Co-occurrence of Sympatric *Poroderma* Species

Population Composition, Trophic Ecology and Movement Behaviour of the endemic *Poroderma africanum* and *P. pantherinum* in Mossel Bay, South Africa.

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Abstract

Species exploiting similar ecological niches are expected to adapt their behaviour, which can either promote or hinder coexistence. This study examined the ecological (dis)similarity between the endemic *Poroderma africanum* (pyjama catshark) and *Poroderma pantherinum* (leopard catshark) in Mossel Bay, South Africa. The co-occurrence of these species was examined along the ecological axes of time, trophic position and space, between October 2015 and April 2018, through the use of Baited Remote Underwater Videos (BRUV), gastric lavage, and acoustic telemetry. Through the deployment of 197 BRUVs, *P. africanum* showed a seasonal, higher Relative Abundance (RA = 0.52), occurring more frequently during winter months, while showing an overall decline in RA over the course of the study period. *Poroderma pantherinum* on the other hand, showed a lower, unseasonal RA (0.20), remaining relatively stable throughout the study period. The BRUV deployments indicated that the two species showed a positive co-occurrence with one other, being sighted in BRUV deployments more frequently together as opposed to in isolation/at random. Acoustic telemetry indicated that the two species were active during different diel periods, influenced by a complex combination of tidal and diel rhythms, while *P. pantherinum* showed a higher residency compared to *P. africanum* (*P. pantherinum*: Continuous Residency Time $(CRT)_{24}$ = 3.32 days (mean), 95% CI: 2.53–4.11 days; *P. africanum*: CRT_{24} = 2.01 days, 95% CI: 1.66–2.36 days). While the two species are sympatric in nature, and have an overlapping, endemic, distribution, acoustic telemetry indicated that

P. africanum showed higher degrees of movement throughout the acoustic receiver array (*P. africanum*: edge density (ED) = 0.25; *P. pantherinum*: ED = 0.12); however, certain areas of the bay showed to be of high importance for both species. Both species revealed high levels of intra- and inter-specific variation in both residency and movement behaviour. Gastric lavage indicated partially overlapping trophic niches, between the two *Poroderma* spp. *Poroderma africanum* had a generalist diet, dominated by teleosts (Index of Relative Importance (IRI)% = 22.69), octopus (IRI% = 11.48) and discarded bait (IRI% = 64.54), while *P. pantherinum* showed indications of being a specialist predator, with a diet dominated by cephalopods (IRI% = 83.68). The two *Poroderma* spp. showed a partially overlapping, but separate trophic niches, while displaying spatial dissimilarity in diet. The study suggests that the two species are able to coexist within the same geographical area through niche differentiation across trophic and temporal ecological axes, with varying spatial use. The intra- and inter-specific differences between the two species may complicate elasmobranch management efforts for these co-occurring endemic catsharks, and as such, efforts should follow either an individual species approach, which is often not feasible, or an ecosystem-based approach, as opposed to considering the genus as a whole.

Contents

List of Abbreviations

Abbreviation	Explanation
AIC	Akaike Information Criterion
ATAP	Acoustic Tracking Array Platform
BRUV	Baited Remote Underwater Video
CC	Clustering Coefficient
CITES	Convention on International Trade in Endangered Species
CRT	Continuous Residency Time
DAFF	Department of Agriculture, Forestries and Fisheries (merged into DEFF in June 2019; renamed to Department of Forestries, Fisheries and the Environment (DFFE) in April 2021)
DEA	Department of Environmental Affairs (merged into DEFF in June 2019; renamed to Department of Forestries, Fisheries and the Environment (DFFE) in April 2021)
DEFF	Department of Environment, Forestries and Fisheries (renamed to Department of Forestries, Fisheries and the Environment (DFFE) in April 2021)
EC	Eigenvector Centrality
ED	Edge Density
F_i	Frequency of particular stomach items in a species i
FFT	Fast-Fourier Transform
FoV	Field of View
GB	Groot Brak
IRI_i	Index of Relative Importance of a species i
IUCN	International Union for Conservation of Nature
KB	Klein Brak
TL	Total Length
MaxN	Maximum Number of individuals of a single species in a BRUV frame over the course of the entire video.
MB	Mossel Bay
MPA	Marine Protected Area
N_i	Number of particular stomach items in a species i
ORI	Oceanographic Research Institute
PCA	Principal Component Analysis
RA	Relative Abundance
RI	Residency Index
SAIAB	South African Institute for Aquatic Biodiversity
SST	Sea-Surface Temperature
TOPS	Threatened or Protected Species
W_i	Weight of particular stomach items in a species i

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Chapter 1

Introduction

1.1 The Three Ecological Axes

The co-occurrence of species is often dependent on the availability of resources and the establishment and use of unique niches by ecologically similar taxa (Kneitel and Chase, 2004). Understanding what drives the co-occurrence of species can in turn provide an understanding of how ecological communities respond to changes in the future (Shipley *et al.*, 2018). If, for example, the co-occurrence is driven by dietary variation, changes in food abundance, either as a result of environmental changes or anthropogenic extraction, could either increase the need for competition, or cause further deviation of dietary niches.

Ecological processes occur along different ecological axes: spatial, temporal, and trophic (Reynolds-Hogland and Mitchell, 2007). Various studies examine sympatric species, i.e., existing in the same geographical area (Mallet *et al.*, 2009), co-existing across the various ecological axes. Spatially the sympatric *Felis margarita* (sand cat) and *Vulpes rueppellii* (Rüppell's fox) show an overlap in space in central Iran, but preferring different habitats within that space (Feizabadi *et al.*, 2018). The sympatric *Sarcophilus harrisii* (Tasmanian devil) and *Dasyurus maculatus* (spotted-tailed quoll), which utilise similar habitats and consume similar prey, were examined across spatial and temporal axes, showing that while *D. maculatus*

did not spatially avoid *S. harrisii*, they were active at different times of the diel cycle, likely to limit encountering *S. harrisii* (Andersen *et al.*, 2020). To examine small-scale trophic separation between sympatric rocky shore crabs *Leptodius exaratus* and *Pilumnopeus convexus*, stable isotope analysis has been used, which indicated that their co-existence was driven by a separation in trophic niches or dietary resource partitioning (Al-Wazzan *et al.*, 2019).

These ecological axes can be extended to identifying a species' ecological niche. By extension a species' foraging niche can be separated into three components according these axes, respectively, feeding location, period of activity, and prey consumed (Spitz *et al.*, 2011). From a population perspective it is shown that species that show a highly specialized, constrained, trophic niche are more likely to be sensitive to changes in prey abundance or composition, while broad, generalized predatory species display higher degree of resilience (Duplisea *et al.*, 2016). However, individual specialisation within these generalist populations would complicate predicting how the overall population would react to changes in food availability (Vander Zanden *et al.*, 2010; Araújo *et al.*, 2011).

1.2 Niche Overlap in Species Communities

While there are various theories and models around ecological processes (Vellend, 2016), as elasmobranchs occur often in abundant sympatric communities, competition is an important aspect to consider within these communities. Competition has been hypothesised to effect the distribution of elasmobranch within a limited geographical area (<20 km; Bethea *et al.*, 2004; White *et al.*, 2004). The ecological role of species varies with food web complexity, the number of trophic redundancies, and the productivity of an ecosystem (Navia *et al.*, 2010). If resources in an ecosystem are limited, it is hypothesized that similar species will compete, resulting in either competitve exclusion (Hardin, 1960), or species and

even individuals adapting as a result of niche plasticity (Niklaus *et al.*, 2017).

Ecological theories dealing with competition include (but are not limited to) niche differentiation, the neutrality hypothesis (Vellend, 2016) and niche plasticity (Niklaus *et al.*, 2017). The niche differentiation hypothesis was the initial theory explaining species coexistence (Schoener, 1974). Species would partition resources along one or more ecological axes, such as trophic, spatial and/or temporal, ensuring lower inter-specific competition compared with the intra-specific competition, resulting in the coexistence of sympatric species. The neutrality hypothesis on the other hand suggests that co-occurring species do not need to differentiate in resource use if their competitive abilities are similar, thus removing the effect of competitive exclusion (Hubbell, 2005). Lastly, niche plasticity refers to the ability of a species to adapt and adjust its ecological niche in response to environmental variations and competitive pressures (Niklaus *et al.*, 2017).

Determining how similar species coexist within the same area has been an important question in community ecology (Schoener, 1974). It is thought that both niche differentiation and neutrality hypotheses explain patterns of species co-occurrence present in nature, with theoretical models highlighting that species can co-exist if they are sufficiently similar or sufficiently dissimilar from each other, leading to patterns of similar species coexisting in the same ecological niches (Scheffer and van Nes, 2006; Vellend, 2016). Sympatric assemblages of predators occupying a similar niche are expected to either exhibit resource partitioning or fine-scale spatio-temporal habitat segregation to reduce the effects of direct competition (Humphries *et al.*, 2016). This can be seen in sympatric *O. orca* populations along the north-east Pacific coastline, where two different population feeding on the same foodsource separate themselves along spatio-temporal lines (Emmons *et al.*, 2021). Competing predators may separate themselves along the previously mentioned ecological axes of space, time or trophic angles, whereby resource partitioning can result in species developing dissimilar diets (Ross, 1986).

The separation of species along ecological axes, as a result of resource partitioning, can in turn be a precursor to evolutionary divergence, as a result of selection pressures generated by interspecific competition (Walter, 1991). This can result in congeneric or morphologically similar species to further diverge evolutionarily.

While habitat segregation or resource partitioning among morphologically similar predators is well studied in terrestrial ecosystems, in marine ecosystems this is still poorly understood (Humphries *et al.*, 2016). This is even more so in the case of co-occurring congeneric predators (Humphries *et al.*, 2016). Recently there has been more of a push towards exploring how co-occurring sympatric elasmobranchs partition resources, for example with stingrays (Yemışken *et al.*, 2018; Mulas *et al.*, 2019), guitarfish (Murillo-Cisneros *et al.*, 2019) and sawfish (Poulakis *et al.*, 2017). However, these studies have primarily relied on exploring resource partioning along a single ecological axis. For example, Yemışken *et al.* (2018) found that *Gymnura altavela*, *Raja asterias* and *Raja clavata* partially segregate their main trophic resources as a mechanism to reduce direct competition in the Mediterranean Sea.

1.3 Ecological Role of Elasmobranchs

Elasmobranchs are known to occupy a variety of trophic levels and use a range of strategies and techniques to locate and capture prey (Cortes, 1999; Heithaus and Vaudo, 2012; Munroe *et al.*, 2018). While elasmobranchs are known for their apex predatory position in the food chain, most elasmobranchs occupy a mesopredatory position, linking the upper and lower trophic levels of the food webs they occupy (Vaudo and Heithaus, 2011). This is especially true for Scyliorhinidae, where the majority of species occupy a mid-level position in their relevant trophic web.

Elasmobranchs can occupy various ecological roles in an ecosystem, such as predators, facilitators, prey, nutrient vectors, or competitors (Heithaus *et al.*,

2022). The ecological role as predator is the most well-known, influencing ecosystems either through direct predation or the risk of predation (fear ecology) they impose (Zanette and Clinchy, 2019). For example, various elasmobranchs are known to influence the abundance and behaviuor of seals around their colonies through direct predation and risk effects (Bowen *et al.*, 2003; Martin *et al.*, 2009; Fallows *et al.*, 2016). Additionally, elasmobranchs may influence an ecosystem as facilitators, whereby they create opportunites for other species to feed without directly being involved. A prime example being pelagic elasmobranchs visiting cleaning stations on reefs or seamounts (Oliver *et al.*, 2011; Murie and Marshall, 2016). With the majority of elasmobranchs occupying a mesopredatory position, it is unavoidable that they end up as prey for higher trophic species, in certain cases other elasmobranchs as well. Even larger bodied elasmobranchs can become prey, such as *Notorynchus cepedianus* (broadnose sevengill shark) and *Carcharodon carcaharias* (white shark) having become prey to *Orcinus orca* (killer whale) around South Africa (Engelbrecht *et al.*, 2019; Towner *et al.*, 2022a,b). The effect elasmobranchs have as nutrient vectors, transferring nutrients from one habitat to another, is still poorly understood, but recent studies have started to investigate such trends (Heithaus *et al.*, 2022). These vectors can include aspects such as carcass deposition, bioturbation, and the excretion and egestion of nutrients. For example, *Carcharhinus amblyrhynchos* (grey reef shark) at an unfished atoll in the central Pacific Ocean were found to act as nutrient vectors for nitrogen transfer from the pelagic environment to foreshore reef habitats (Williams *et al.*, 2018). Part of further developing the understanding of the role elasmobranchs may have on bottom-up processes involves developing a more quantitative framework that intergrates movement ecology, foraging, and digestive physiology (Earl and Zollner, 2017; Heithaus *et al.*, 2022).

World-wide there is high species diversity of chondrichthyans with over 1600

known species (Ebert *et al.*, 2021a). Some locations are well known to have a high degree of co-occurance and can be considered "hotspots" for chondrichthyan diversity (Derrick *et al.*, 2020). The southern African coast is one of several areas in the world with a high chondrichthyan richness (Derrick *et al.*, 2020), representing nearly 15% of all known chondrichthyans (Ebert *et al.*, 2021b) (of these 59 species are endemic to the area; Ebert and van Hees, 2015). With such a high degree of richness, it is unavoidable that niche overlap can occur between sympatric species.

1.4 Scyliorhinidae

Scyliorhinidae[1] were until recently the largest and most diverse elasmobranch family in the world (Ebert *et al.*, 2021a). The group has now been split into Scyliorhinidae (catsharks) and Pentanchidae (deepsea catsharks) based on the presence or absence of an internal 'crest' over the orbits of their eyes, respectively (Ebert and Dando, 2020).Many of the scyliorhinidae genera are morphologically conservative, having a cylindrical shape, tapering at either end (fusiform; Compagno, 1988), which contrasts with their paraphyletic origins (Human *et al.*, 2006). Scyliorhinidae have moderately large spiracles, a vestigial gill opening behind the eyes, five pairs of gill slits, and elongated, cat-like eyes that are situated high on the sides of the head.

Scyliorhinidae are generally small, with the majority less than 80 cm Total Length (TL). The most predominant exception is *Scyliorhinus stellaris* (nursehound), which reaches up to 162 cm TL (Ebert *et al.*, 2021a).

1.4.1 Scyliorhinidae Distribution

Scyliorhinidae have a worldwide distribution and can be found from tropical waters to cold temperate latitudes, and from the intertidal zone down to 2000 m

[1]Upper-case to define the specific family; Lower case to specify catsharks in general.

depth (Compagno, 1984). Despite their high diversity and worldwide distribution, ecological information of scyliorhinidae, such as habitat utilisation and movement behaviour, remain poorly known (Awruch *et al.*, 2012).

Many species of Scyliorhinidae (and the recently split-off family Pentanchidae) in southern Africa are common to abundant, including species from the genera *Halaelurus, Haploblepharus, Holohalaelurus, Poroderma* and *Scyliorhinus*. Southern Africa has several endemic scyliorhinidae with a total of two endemic genera, 13 endemic species and several near endemics (Human *et al.*, 2006). Out of the 19 different species present in southern Africa (Ebert and van Hees, 2015), inshore Scyliorhinidae/Pentanchidae fauna of the Western Cape is limited to *Poroderma* spp. (2 species), *Haploblepharus* spp. (4 species), and *Halaelurus natalensis* (tiger catshark) (Pretorius and Griffiths, 2013). Mossel Bay, the study area of this work, is home to *Poroderma* spp., *H. natalensis*, and *Haploblepharus edwardsii* (puffadder shyshark). Little research has been done on these southern African scyliorhinidae species, most likely due to their small size and lack of commercial value.

1.5 *Poroderma* spp.

The genus *Poroderma* is a stocky, compressed scyliorhinid with clearly visible anterior nasal flaps (Ebert *et al.*, 2013). It is the only genus in Scyliorhinidae with distinctive conical barbles (Compagno, 1999). While the Scyliorhinidae family is paraphyletic, *Poroderma* (and *Scyliorhinus*) are monophyletic (Human *et al.*, 2006). *Poroderma* spp. are predominantly benthic and endemic, found on rocky reefs around the south and east coast of South Africa. Anecdotal and mark-recapture studies suggest that the *Poroderma* spp. have a limited home range and are philopatric (Dainty, 2002; Human, 2006b; Escobar-Porras, 2009).

Genetically the two *Poroderma* spp. are very closely related (van Staden, 2018; van Staden *et al.*, 2023).

1.5.1 *Poroderma africanum*

Poroderma africanum Gmelin 1789, commonly known as the pyjama catshark[2], is one of the two species in the *Poroderma* genus. The species is light to dark grey in colour, with thick black longitudinal stripes across the entire length of its body (Figure 1.1). The nasal barbels are prominent, yet short.

The distribution of *P. africanum* ranges from Saldanha Bay, in the Western Cape, to East London, in the Eastern Cape (Human, 2006b), with its highest concentration along the Western Cape coastline (Heemstra and Heemstra, 2004; Pretorius and Griffiths, 2013; Figure 1.2). The species is found on rocky reefs, often in caves, down to a depth of 108 m depth (Ebert *et al.*, 2021a) and is suggested to be nocturnal (Compagno *et al.*, 2005).

Poroderma africanum has an oviparous reproduction cycle, laying one egg per oviduct (Compagno *et al.*, 1989), and females are believed to lay eggs throughout the year (Compagno, 2017). Embryos hatch at a size of ∼14 cm TL and reach a maximum size of 109 cm TL (Ebert *et al.*, 2021a). The maximum weight was recorded at 7.9 kg (van der Elst, 1993).

The length at 50% maturity (L_{50}) is still disputed, with multiple sources providing different lengths (Table 1.1). The age at maturity of *P. africanum* is estimated to be around 10 to 13 years (Compagno, 2017), and as a result the generation period of *P. africanum* is estimated to be 25 years (Pollom *et al.*, 2020a).

[2]Synonyms: pyjama shark, striped catshark

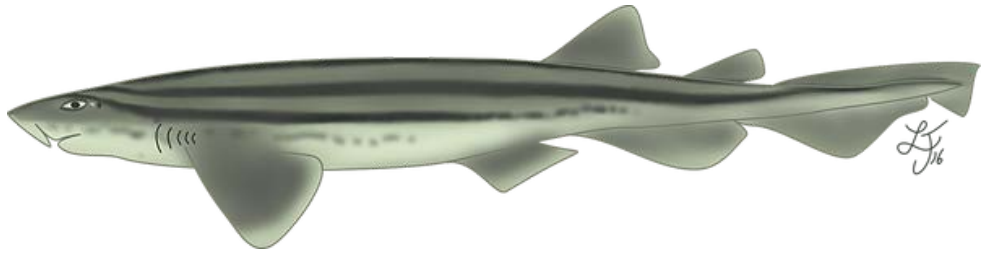


Figure 1.1: Illustration of *Poroderma africanum* showing distinctive horizontal black stripes. Source: Elasmo-Africa.

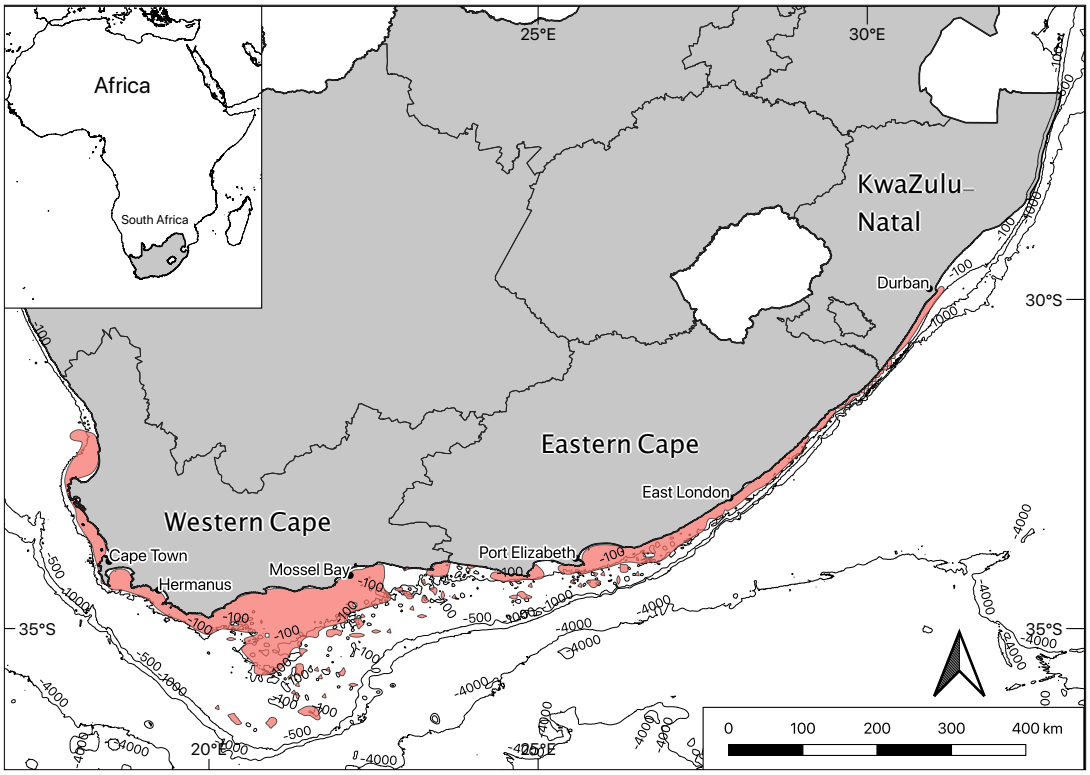


Figure 1.2: Distribution map of *P. africanum* (light red) along the South African coastline, with coastal towns and provinces as mentioned in text. Source: Pollom *et al.* (2020a). Created with qGIS v3.12.

Table 1.1: Length at 50% maturity (L_{50}) of *P. africanum* according to various sources and by location.

Source	Location	Males	Females
Bass *et al.* (1975)	East Coast of South Africa	580-760 mm	650-720 mm
Roux (2002) (*BSc Honours*)	Eastern Cape	845 mm	885 mm
Dainty (2002) (*MSc*)	Western Cape	857 mm	849 mm
Ebert *et al.* (2021a)	South Africa	720 mm	780 mm

1.5.2 *Poroderma pantherinum*

Poroderma pantherinum Müller & Henle, 1838, commonly known as the leopard catshark, is the other species belonging to the *Poroderma* genus. It displays several different colour morphs, ranging from light to dark brown with patterns of leopard-like rosettes to small or large black spots and partial longitudinal lines (Compagno *et al.*, 2005; Figure 1.3). A previously identified species (*Poroderma marleyi*, blackspotted catshark; van der Elst and Vermeulen, 1986) is now considered a colour-variant of *P. pantherinum* (Human, 2006b). The nasal barbles are longer than *P. africanum* and reach the mouth (Compagno *et al.*, 2005).

Its distribution ranges from Cape Town in the Western Cape, to Durban in KwaZulu-Natal (Human, 2006b) and is found in higher concentrations around the Eastern Cape (Heemstra and Heemstra, 2004; Pretorius and Griffiths, 2013; Figure 1.4). The species is found to depths up to 274 m (Ebert *et al.*, 2021a).

Poroderma pantherinum follows the same reproduction mode as *P. africanum* (oviparous, one egg per oviduct; Compagno *et al.*, 1989). One individual was observed hatching at 11 cm TL (Dainty, 2002; Ebert *et al.*, 2021a). The length at 50% maturity ranges around 61 cm TL for males, and 51 cm TL for females (Ebert *et al.*, 2021a), with the age of maturity for both sexes at 10 to 17 years (Roux, 2002; Mann, 2013). The maximum size is 77 cm TL (Ebert *et al.*, 2021a), with a maximum age of 19 years (Dainty, 2002). As a result the generation period for *P. pantherinum* was estimated to be 22 years (Pollom *et al.*, 2020b). The maximum

recorded weight is 3.2 kg (van der Elst, 1993).

The two species are morphologically very similar, with their primary morphological differences being size and colour pattern. In general the color patterns of scyliorhinidae are highly adapted for camouflage. Camouflage is utilized both for ambushing prey and predator avoidance, and is often used in combination with behavioural adaptations (Stevens and Ruxton, 2019). Crypsis is a form of camouflage in which all traits reduce the risk of an animal being detected visually by a predator (Stevens and Merilaita, 2009). The mottled and spotted patterns of scyliohinidae help the species blend in with their surroundings (i.e. background matching), as seen with *P. pantherinum* and other sympatric scyliorhinidae in the area such as *Haploblepharus* spp. However, the striped pattern of *P. africanum*, similar to those seen in zebras (*Equus* spp.) (How and Zanker, 2014), suggests either a motion dazzle function, preventing the accurate estimates of speed and direction by the observer (predator) (Stevens and Ruxton, 2019), or disruptive colouration, breaking up the body outline (Skelhorn and Rowe, 2016; Barnett *et al.*, 2017).

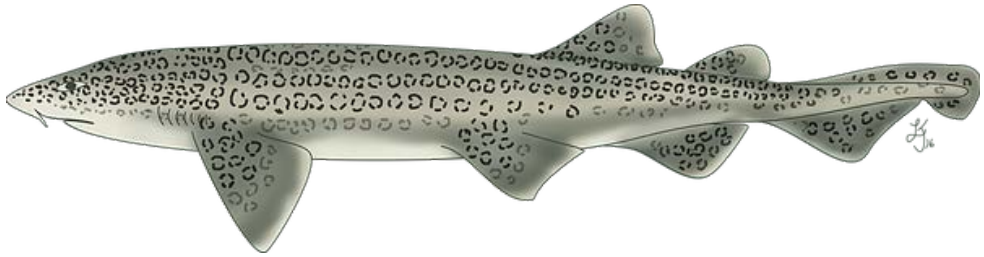


Figure 1.3: Illustration of *Poroderma pantherinum* showing distinctive leopard-like rosettes. Source: Elasmo-Africa.

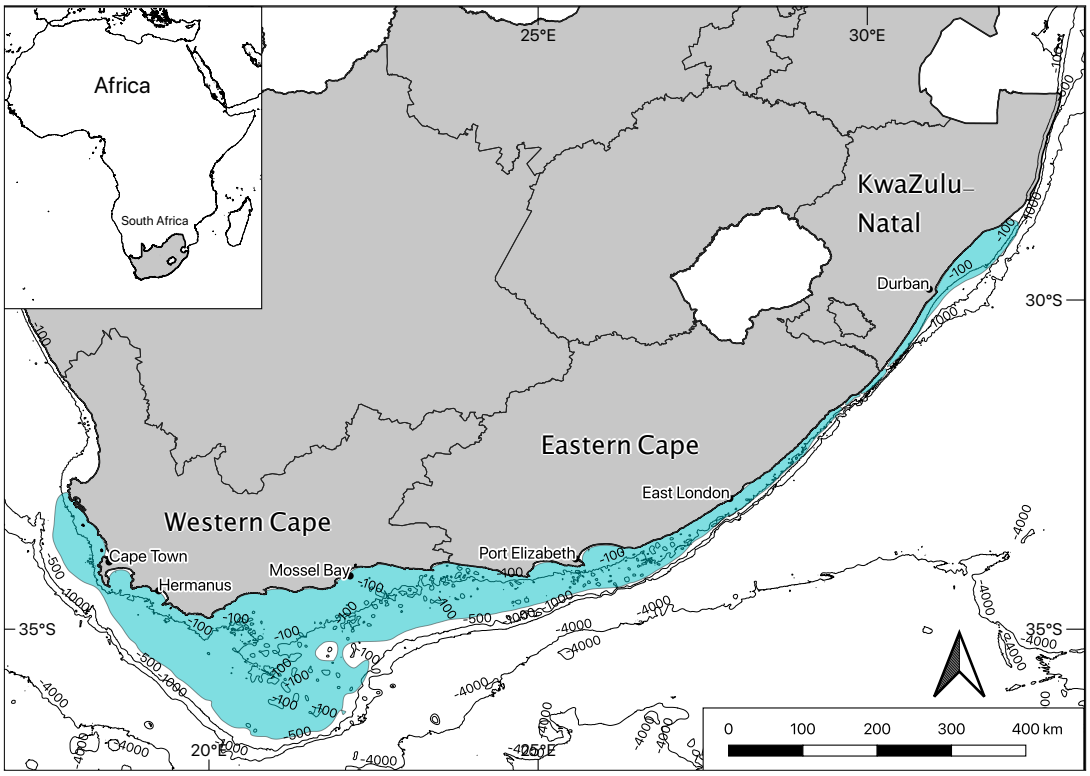


Figure 1.4: Distribution map of *P. pantherinum* (light blue) along the South African coastline, with coastal towns and provinces as mentioned in text. Source: Pollom *et al.* (2020b). Created with qGIS v3.12.

1.6 Conservation Concerns Surrounding Elasmobranchs

Overfishing has resulted in population declines of larger elasmobranchs around the world (Dulvy *et al.*, 2014), with mass-removal of these apex predators having detrimental effects further down the trophic web (Sherman *et al.*, 2020). Their removal has implications for mesopredators as a result of a subsequent trophic cascade, whereby the increase in abundance of the primary prey of the apex predator results in higher predation on lower-level predators (Heithaus *et al.*, 2008). The regional effects of species' declines can be explored only where adequate information regarding the abundance, diversity and distribution of chondrichthyans is available (Ferretti *et al.*, 2010; McCauley *et al.*, 2012; Ruppert *et al.*, 2013; White *et al.*, 2014).

Several main threats identified for chondrichthyans are overexploitation through targeted fisheries and by-catch, habitat degradation, persecution (e.g., shark culling), and climate change (Dulvy *et al.*, 2014), and several shark species have been listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

1.6.1 *Poroderma* spp. in a Conservation Context

Poroderma spp. are affected by at least two of the main conservation threats identified by Dulvy *et al.* (2014), namely by-catch (Attwood *et al.*, 2011; da Silva *et al.*, 2015) and persecution (van der Elst, 1993; Human, 2006b). Habitat loss and climate change affect ecosystems around the South African coast (Moloney *et al.*, 2013), which can indirectly influence catshark populations further around southern Africa.

In 2017, both *Poroderma* spp. were placed by the South African government on

the Threatened Or Protected Species (TOPS) list (DEA 2017a). The two *Poroderma* spp. were downgraded to Least Concern on the International Union for the Conservation of Nature (IUCN) Red List in 2019 from Near Threatened and Data Deficient for *P. africanum* and *P. pantherinum*, respectively (Pollom *et al.*, 2020a,b). The initial assessment was due to their limited distribution, heavily utilised habitat, and the threat of the populations from recreational fishing pressures (Compagno, 2017; Human, 2017). In addition, the population of *P. pantherinum* is suspected to be fragmented, causing greater risk to their population persistence due to limited gene flow (Bester-van der Merwe and Gledhill, 2015). The new assessment was based on recreational angling data from De Hoop Marine Protected Area in the Western Cape, approximately 150 km west of the study site (Pollom *et al.*, 2020a,b). As the generation lengths for *P. africanum* and *P. pantherinum* are 25 and 22 years, respectively, and the MPA has been in place for 20 years (DEA 2020), the two species would have had a generation of protection from exploitation.

Due to the species distribution along the South African coastline but with populations seemingly being locally influenced, the lack of ecological data and how the species would respond to these influences is problematic. While da Silva and Kerwath (2022) indicates an increasing population trend for both species, the report's referral to the species' recent IUCN status (Pollom *et al.*, 2020a,b) makes it unclear whether this is based on the De Hoop MPA capture data or not. In contrast to the findings from De Hoop MPA, a local population study in Mossel bay showed a downward population trend for *P. africanum* (Grusd *et al.*, 2019). The shifting population dynamics that coincide with the identified threat pressures requires a better understanding of the species' ecology, how the two species interact with each other, and what influences the species interactions with the environment.

1.7 Purpose of This Study

Poroderma africanum and *P. pantherinum* are sympatric, occupying the same habitat within the same overlapping distribution, and are thought to have a similar diet (Heemstra and Heemstra, 2004; Ebert *et al.*, 2013, 2021a). The two species are morphologically very similar, with their primary morphological differences being size and colour pattern. With such morphological, distribution and apparent trophic similarities, this questions whether their ecologies are similar enough to fall under Schoener (1974)'s theory of niche differentiation or Hubbell (2005)'s hypothesis of neutrality.

As spatio-temporal patterns of species abundance influence the strength of trophic interactions between and amongst different layers of the trophic web, the movement of both predators and prey helps determine those patterns of abundance (Andrews and Harvey, 2013). The purpose of this study was to examine how *P. africanum* and *P. pantherinum* co-exist within the Mossel Bay area through a multi-axis ecological examination. Through the use of three different techniques, the three ecological axes of time, food and space are explored with a focus on the *Poroderma* spp.

While niche differentiation suggests that species partition resources along various ecological axes, usually only one axis is explored in studies exploring niche breadth differences between species (Pianka, 2000; Rotkopf *et al.*, 2012). Past studies have examined various aspects of the ecology of these species (Dainty, 2002; Escobar-Porras, 2009; Roux, 2002; Meyer, 2017), however, peer-reviewed publications are limited (e.g., Haywood, 1973; Human, 2006a,b; Pretorius and Griffiths, 2013), and often the results were part of broader investigations of species assemblages (e.g., Lamberth, 2006; Lechanteur and Griffiths, 2002; Attwood *et al.*, 2011; Oliver *et al.*, 2015; de Vos *et al.*, 2015). This is the first study to investigate the genus as a whole, to examine various aspects of their ecology and behaviour using integrated

and varied techniques to better understand the complexities of these co-occurring species relative abundance, diet composition, and movement behaviour.

The specific objectives of this study were as follows:

i) To assess the ichthyofaunal assemblage of the Mossel Bay reefs and assess temporal variation in relative abundance of the *Poroderma* spp. This was achieved using Baited Remote Underwater Video (BRUV) deployments at three target reefs in the Mossel Bay area. The diversity and relative abundance of each species were determined, correlated with environmental variables, and the co-occurrence between each species was explored.

ii) To determine the trophic ecology of the *Poroderma* spp. and examine spatial variation in diet in Mossel Bay and Walker Bay. Stomach content was collected from both species using gastric lavage, and items were classified as closely to species level as possible. Differences in diet between the two species, sexes, and locations were explored, and the trophic position determined.

iii) To examine the movement behaviour and space use of the *Poroderma* spp. in Mossel Bay by conventional tagging and passive acoustic telemetry. A historical dataset was used to explore the nationwide movement behaviour of conventionally tagged *Poroderma* spp. For acoustic telemetry, individuals of both species were surgically implanted with transmitters and tracked over a network of 18 acoustic receivers.

Investigating the ecological knowledge gaps surrounding these two species will provide insights into the coexistence of sympatric shark species by identifying key areas of temporal variation in abundance within ecology communities (Chapter 3), variation in trophic roles (Chapter 4), and space use within a small embayment (Chapter 5), which can inform conservation and management strategies to promote long-term sustainability of endemic shark populations. It is expected that these species separate themselves along one or more of the previously mentioned ecological

axes, and have divergent niches that allow them to coexist within the same ecosystem without strong competition.

1.8 Thesis Structure

The subsequent chapters of this thesis are set out as follows:

Chapter 2 will provide a description of the study site, background information on the various techniques used in this study, and an explanation of the major techniques used in this study.

Chapter 3 examines the overall community structure and dynamics of the assemblage, as well as how environmental factors influence the abundance and representation of two *Poroderma* spp. within the ichthyofaunal assemblage of Mossel Bay.

Chapter 4 explores the differences in the diet composition and trophic interactions of the two *Poroderma* spp., as well as how individual traits such as sex and size shape feeding ecology between habitat and environmental conditions.

Chapter 5 assesses the movement patterns and space use of the two *Poroderma* spp. through conventional tagging and passive acoustic telemetry, and explore intra-specific differences along temporal and spatial scales.

Chapter 6 synthesizes the information from all prior chapters and discusses the significance of these findings along the ecological axes, identify how these two species co-exist, and the impact this has on their conservation.

1.9 Ethics Clearance

This thesis was performed following permit conditions laid out by DEA/DAFF (permit number RES2015/21) and ethically cleared by the South African Institute for Aquatic Biodiversity (SAIAB; ethics number 2015_05).

Chapter 2

General Methods

2.1 Study Areas

Mossel Bay was selected as the main study site due to the known presence of the *Poroderma* spp. (Chapters 3 and 4), located centrally within the distribution ranges of both species, the presence of inshore reef systems (Chapter 3), and the existing acoustic receiver array (Chapter 5). Walker Bay was selected as a secondary study site to examine spatial variation in diet composition (Chapter 4), and was determined to be a suitable comparison site due to similarities in the ecosystem. Both sites are located in the Western Cape Province of South Africa (Figure 2.1), and are located within the warm-temperate Agulhas marine bioregion (Lombard *et al.*, 2004). This area sits at the most southern point of the continent of Africa, and is influenced by two major oceanic currents: The warm Agulhas Current coming from the Indian Ocean, flowing down South Africa's east coast; and the cold Benguela Current, coming up from the Southern Ocean and flowing along South Africa's west coast. This causes the average Sea Surface Temperatures (SST) around southern Africa to range from 13 °C in Luderitz (Namibia), to 27 °C along the KwaZulu-Natal Bight (Carr *et al.*, 2021).

2.1.1 Mossel Bay

Mossel Bay (34°08' S, 22°07' E) is situated on the southern coast of the Western Cape, South Africa. It is a shallow, semi-enclosed bay with substrata consisting mostly of sand, with various patches of sandstone reef close inshore (Figure 2.2, Cawthra *et al.*, 2016).

The Cape St. Blaize peninsula protects the inner bay on the south-western side from prevailing weather. Seal Island, a rocky outcrop, is located near the western side of the bay, 800 m from the nearest shore, Diaz Beach. A colony of *ca* 4 500 *Arctocephalus pusillus pusillus* (Cape fur seals) reside on Seal Island (D. Kotze, pers. comm.), which is a provincial nature reserve (DEA 2020) and is one of four main established *Carcharodon carcharias* (white shark) aggregation sites in South Africa (Kock and Johnson, 2006).

Mossel Bay has one of the eight commercial harbours in South Africa with moorings for trawlers, long-liners and line-fishing boats. There are two off-shore mooring sites (-34°08.65', 22°07.73'; -34°08.64', 22°08.48') within the port limits with a 500 m no-go zone. There is a long history of commercial and recreational fishing in the area and the town developed significantly since the 1980s due to the discovery and exploitation of off-shore petroleum gas fields (De Kock Associates and Delia Power Town Planning Services, 2013). The presence of a harbour and history of industrial, commercial and recreational fishing, together with offshore gas exploration and other commercial activities makes Mossel Bay an anthropogenically impacted marine area. The presence of the various types of fishing practices introduces the possibility of fishing discards entering the ecosystem (Goñi, 1998), thus potentially altering the ecosystem functioning by introducing alternative food sources to predators (Jenkins *et al.*, 2004).

Three reefs were selected where upon primary effort was focused: Roman's Reef, Mitch Reef and Darwin Reef. These reefs had similar reef profiles and were composed

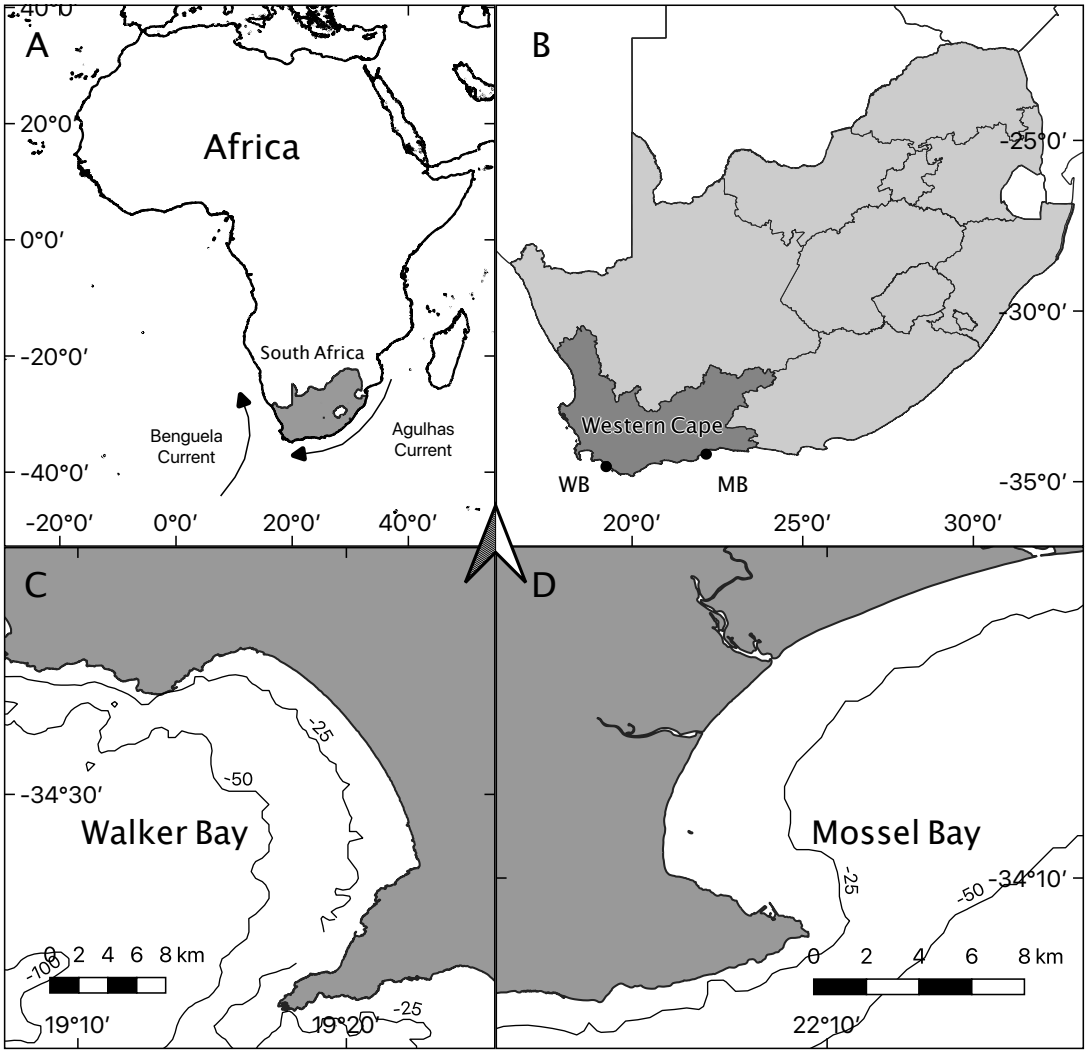


Figure 2.1: (A) Location of South Africa with Africa, (B) the Western Cape within South Africa, with Mossel Bay (MB) and Walker Bay (WB) highlighted, (C) the study sites of Walker Bay, and (D) Mossel Bay. Created with qGIS v3.12.

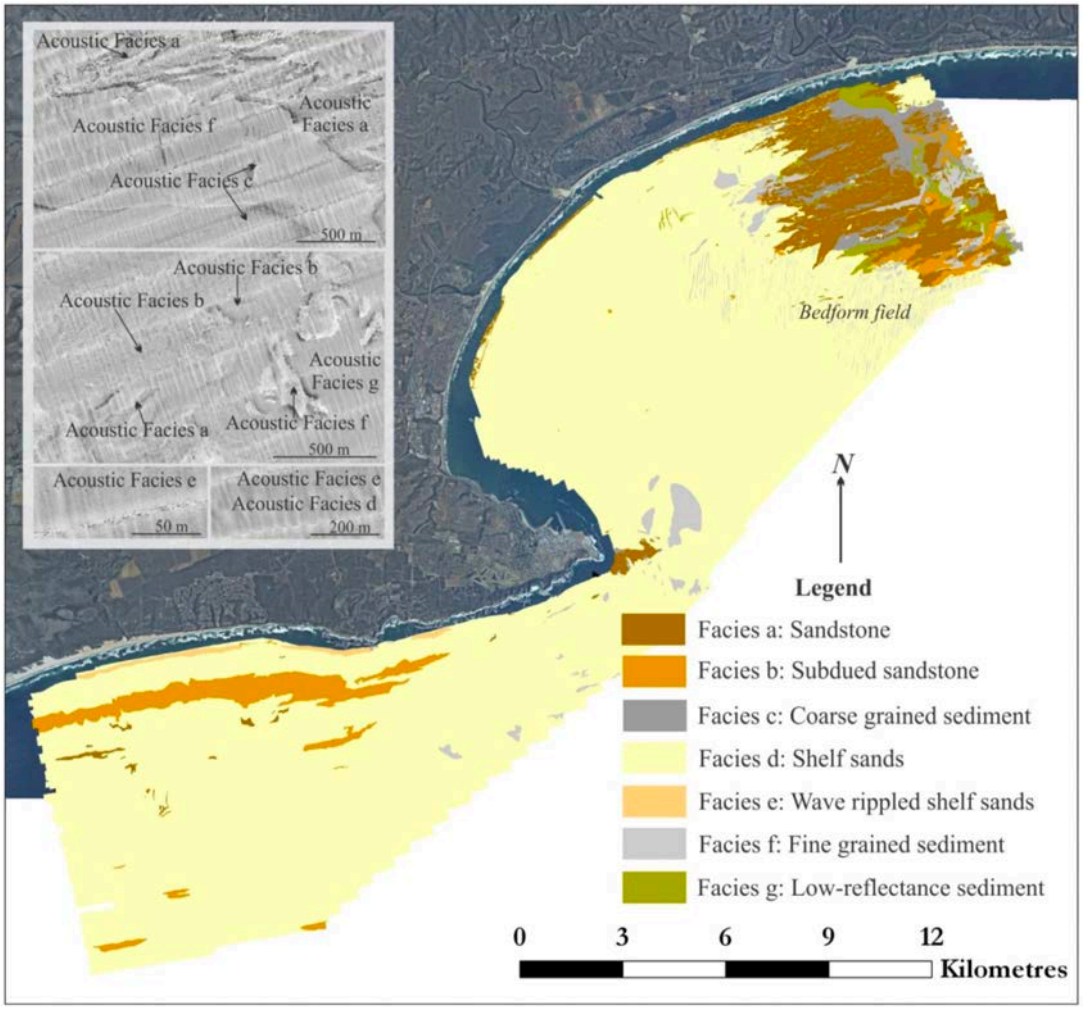


Figure 2.2: Distribution of interpreted acoustic facies characterising the seafloor of Mossel Bay. Source: Cawthra (2014), used with permission.

of Table Mountain Group sandstone (Cawthra, 2014). These reefs were selected due to their accessibility, the known presence of the target *Poroderma* spp., and their proximity to one another to allow for the examination of their movement behaviour (Chapter 5). With the exception of the provincial nature reserve of Seal Island, the area is unprotected.

2.1.2 Walker Bay

Walker Bay is an open bay located between Cape Town and Cape Agulhas. A local fishing town, Hermanus, is located along the northern edge of the bay (-34°25.2'; 19°14.55'; Figure 2.1). Walker Bay is located approximately 270 km west of Mossel Bay, and 95 km southeast of Cape Town. Located in the same biogeographic region as Mossel Bay, the area is more influenced by the Benguela Current. The benthic structure of the bay is composed of a large central reef system, with sand substratum along the north, east, and southern part of the bay (Lenhoff, 1995), and the coastline along the northern shore of the bay has large patches of kelp forests (Osgood *et al.*, 2019). A large, seasonal Marine Protected Area (MPA) is located along the inner 113 km^2. Established in 2001, the Walker Bay Whale Sanctuary (WBWS) was created to protect *Eubalaena australis* (Southern right whale) and is in effect between July and December. During this time all vessels are prohibited, except for whale watching vessels (Osgood *et al.*, 2019).

2.2 Research Methods

2.2.1 Baited Remote Underwater Video Surveys

With the increased concerns over the status of some threatened, endangered and protected species, extractive methods have become less ethically acceptable when examining shark abundance and diversity (Harvey *et al.*, 2019). Determining the

abundance of an ecologically vulnerable species, the use of a non-lethal, non-destructive sampling method is advantageous to the conservation of the species (Cappo *et al.*, 2007).

Visual surveys, conducted via SCUBA divers, have been widely accepted to provide an acceptable estimate of relative and possible absolute abundance of marine biodiversity (Connell *et al.*, 1998). However, many shark species are rare, highly mobile, nocturnal, or behaviourally influenced in their response to divers, creating a sampling bias in their assessments (MacNeil *et al.*, 2008),

The use of Remote Underwater Video (RUV) camera systems to complete underwater observations has provided an alternative to relying on divers for identification and counting. RUVs can reach depths and habitats often inaccessible to divers (Goetze *et al.*, 2011), and avoid behavioural response biases towards divers by fish (Watson and Harvey, 2007; McCauley *et al.*, 2012). Remote underwater visual surveys can sample for longer periods regardless of the time of day, however, as nocturnal visual surveys are reliant on a light source, can influence the diversity sighted at night during the survey (Harvey *et al.*, 2012). Additionally, the footage can also be stored as a permanent digital record (Cappo *et al.*, 2003). As the system is visual based, the method is reliant on good visual circumstances to provide an effective results, and is biased towards cryptic species (Colton and Swearer, 2010; Lowry *et al.*, 2012).

Theoretically, unbaited stationary cameras should be able to track the true abundance of fish, including sharks and rays, in a study area (Harvey *et al.*, 2019). However, sharks generally occur in low densities and being highly mobile, requires an exceptionally large sample size for unbaited camera stations compared with baited camera stations to be compared with baited camera stations to allow for robust statistically comparisons. For this reason, unbaited stationary cameras are used in a limited capacity (Harvey *et al.*, 2019). A solution is to provide some form of attractant to increase the number of animals in the Field-of-View. The act of

adding bait to the RUV system turns the rig into a Baited Remote Underwater Video (BRUV) system.

The first BRUV system was developed in 1995 (Ellis, 1995), before further development by Babcock in the late 90s (Babcock *et al.*, 1999; Willis and Babcock, 2000) and Cappo in early 2000 (Cappo *et al.*, 2003, 2004). BRUVs have been used to study fish community structures in MPAs (Willis *et al.*, 2000; de Vos *et al.*, 2014; Albano *et al.*, 2021), deep-sea habitats (Marouchos *et al.*, 2011) and structurally complex marine environments, such as coral reefs (Stewart and Beukers, 2000). Compared with other research methods for assessing marine communities, BRUVs are non-invasive, non-destructive, not size-selective, applicable at any depth, and cause negligible damage to the benthic environment. BRUVs can detect large, mobile animals that normally avoid divers and other active fishing surveys (Cappo *et al.*, 2007). BRUV surveys have gained international popularity and application in recent years and have been used successfully to assess fish communities across the globe, including the western Indian Ocean (Clarke *et al.*, 2012), Australia (Meekan and Cappo, 2004), Florida, the Cayman Islands and Belize (Brooks *et al.*, 2011), and South Africa (e.g., Bernard and Götz, 2012; de Vos *et al.*, 2014; Osgood *et al.*, 2019; Albano *et al.*, 2021).

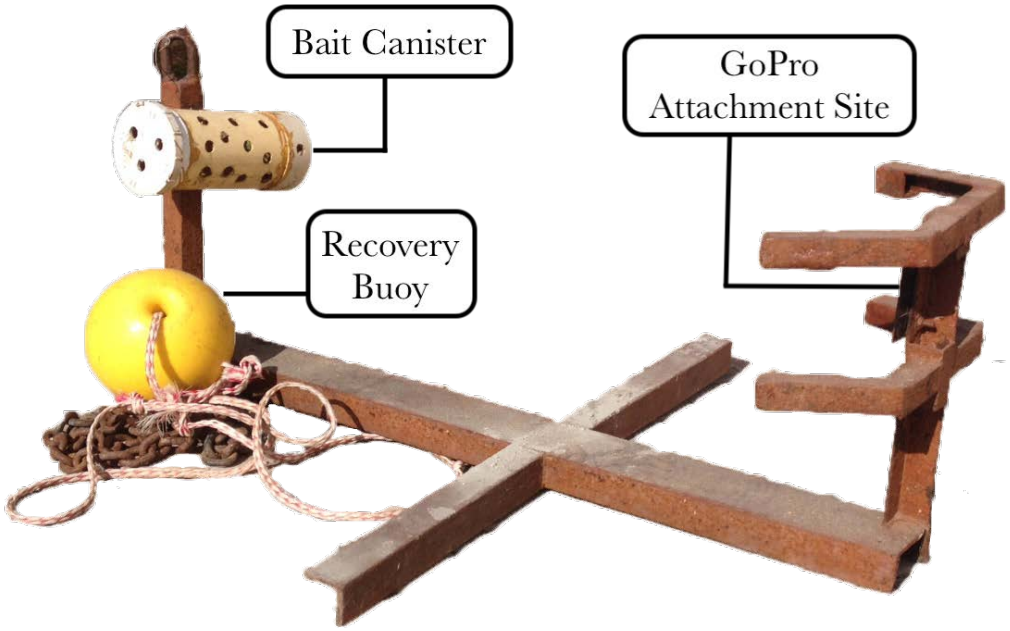


Figure 2.3: Image of the BRUV rig with the bait canister, GoPro attachment site, and recovery buoy featured.

The BRUV rig used for this study is a steel structure with a GoPro Hero 3 attached to one end, approximately 30 cm off the ground, and a perforated bait canister filled with *Sardinops sagax* (sardines) at the other end, one metre from the camera (Figure 2.3). The rig had a horizontal cross-bar for stabilisation connected by a chain and rope to a buoy for surface retrieval. The camera was fixed to ensure the bait canister is in the centre of the Field-of-View.

2.2.2 Gastric Lavage

In the past, trophic studies have primarily used lethal sampling methods (Kamler and Pope, 2001; Barnett *et al.*, 2010b). However, increased ethical considerations for sharks, as well as the conservation status of many shark species being listed as either Threatened or Data Deficient (including the *Poroderma* spp. at the start of this study), has led to the use of alternative non-lethal sampling methods (Hammerschlag and Sulikowski, 2011; Bangley *et al.*, 2013).

A variety of non-lethal sampling methods have been used for chondrichthyans,

including the sampling of stomach contents through stomach eversion. This involves anaesthetizing the shark, reaching into the stomach with a pair of forceps, and inverting the gut content out of the mouth into a collection tray (Cortés and Gruber, 1990). This mimics the shark's natural ability to evert its entire stomach without permanent damage (Brunnschweiler *et al.*, 2005).

Another method is by flushing the stomach of the animal, also known as gastric lavage and allows for the sampling of an animal's stomach content with minimal equipment (Bangley *et al.*, 2013). The method involves pumping water into the stomach through a tube until all the food items are expelled via the mouth (Barnett *et al.*, 2010b). The principle of gastric lavage was first developed by White (1930) to collect stomach contents from *Salvelinus fontinalis* (brook trout) by inserting a glass tube into the stomach and applying pressure from the outside. This method has been performed on a variety of faunal groups and species, including *Mirounga angustirostris* (elephant seals; Antonelis Jr. *et al.*, 1987), sea turtles (Eckert *et al.*, 1999), a large variety of teleosts (Hartleb and Moring, 1995), and elasmobranchs (Vaudo and Heithaus, 2011; Ajemian *et al.*, 2012; Elston *et al.*, 2015).

While this method is non-lethal to the animal, it can be a highly stressful and invasive procedure. Nevertheless, the information on prey consumption and thus the feeding habits and ecological role of sharks in their respective ecosystems can provide valuable information for research and conservation efforts. Therefore it would need to be conducted in a responsible and ethical manner to minimize any harm to the animal.

Due to the effects of digestion, stomach content analysis provides information on prey items that have recently been consumed. While the occurrence of unidentifiable items as a result of digestion could hinder analysis (Vander Zanden *et al.*, 1997; Richardson *et al.*, 2000; Pinnegar *et al.*, 2001; Renones *et al.*, 2002), and digestion-rates of different prey items could over-estimate the importance of certain items (van der Heever, 2017), these disadvantages are outweighed by the

non-lethal nature of the method.

Other methods such as stable isotope analysis, fatty acid amides, or eDNA are available to study the diet and feeding habits of sharks, each dependent on the research questions, available resources, and ethical considerations.

Stable isotope analysis relies on the intergration of isotopes into a consumer's tissues over time. This can provide long-term estimates of the diet of the target species, and avoids the 'snapshot' bias associated with stomach content analysis (Hussey *et al.*, 2012a; Shiffman *et al.*, 2012). However, this method is limited in its ability to identify specific prey items or to determine the frequency of feeding events (Hussey *et al.*, 2012a; Shiffman *et al.*, 2012; Munroe *et al.*, 2018). Fatty acid amides are compounds that are produced in the body of an animal in response to the ingestion of specific types of prey (Couturier *et al.*, 2020). However, this method is limited by the detectable quantities in the tissues of a shark, and is unable to identify specific prey items (Munroe *et al.*, 2018). Environmental DNA, or eDNA, involves the detection of genetic material from the environment to determine the presence of specific prey species (Le Port *et al.*, 2018). While this method is non-invasive and can provide information about the presence of prey items in the environment, unless feacal samples are collected, it cannot provide information about the feeding habits or frequency of feeding events of the shark (Nørgaard *et al.*, 2021). Compared to stable isotope analysis, fatty acid amides, and eDNA, gastric lavage can provide more specific and detailed information about the diet and feeding habits of sharks.

2.2.3 Passive Acoustic Telemetry

The development of electronic devices capable of recording aquatic animal movements allows for the monitoring of elasmobranchs in their natural habitats in greater detail. Acoustic telemetry has been used around the world by researchers to look into the movement, home range, residency (Heupel and Webber, 2012; Stocks

et al., 2015) and management enquiries of species. It has been used in a multitude of studies to track the movement of species such as crustaceans (MacArthur *et al.*, 2008; Wiig *et al.*, 2013), cephalopods (Pecl *et al.*, 2006; Sakai *et al.*, 2017), teleosts (Lembo *et al.*, 1999; Govinden *et al.*, 2013), chondrichthyans (Barnett *et al.*, 2011; Matich and Heithaus, 2014; Cagua *et al.*, 2015), and more relevantly, Scyliorhinidae (Awruch *et al.*, 2012; Jacoby *et al.*, 2012; Sims *et al.*, 2005).

Passive acoustic telemetry is based on the principle of attaching a transmitter, that sends an acoustic signal, to a study animal; and a receiver that can detect the signal if the animal comes within range. It was first developed in 1956 to actively track salmon movement at the Bonneville Dam on the Columbia River (Trefethen, 1956; Hockersmith and Beeman, 2012). Over the years acoustic telemetry has rapidly evolved into a powerful tool for observing marine animals in coastal and continental shelf ecosystems (Hussey *et al.*, 2015). This was enabled by the development of receivers that were autonomous and self-contained, allowing for the recording and storing of large amounts of data over periods of months (Klimley *et al.*, 1998; Kessel *et al.*, 2014). Detections of tagged animals were recorded in the memory banks of the receiver, after which the receiver would be retrieved and the data downloaded (Heupel *et al.*, 2006).

As the *Poroderma* spp. are relatively small, benthic in nature, do not break the water surface like other more pelagic species, and does not have a rigid dorsal fin like Lamnids or Requiem shark species, other transmitter options such as satellite or PAT transmitters were considered detrimental to the survival of the individuals and would not provide an accurate measure of the natural movement behaviour of the *Poroderma* spp. (Heupel *et al.*, 2018a).

2.3 Animal Capture and Handling

Examination of the stomach content through gastric lavage (Chapter 4) and the surgical insertion of acoustic transmitters (Chapter 5) required the capture of live animals. Individuals were captured using primarily rod and reel, or traps, from a boat in Mossel Bay (Chapters 4 and 5), while in Walker Bay most samples were caught from shore along Hermanus (Chapter 4). Various baits were used, including (but not limited to) *Scomber japonicus* (chub mackerel), *S. sagax*, *Octopus vulgaris* (Common octopus), and *Sepia* spp. (squid). Boat capture allowed for a shorter fight time, limiting the possibility of stomach eversion. Furthermore, to limit air exposure which could increase blood lactate levels (Butler *et al.*, 2017; Scarponi *et al.*, 2021), captured individuals were immediately placed in a container with fresh seawater. Before performing the gastric lavage (Chapter 4), it was noted whether the bait was retrieved or not.

2.3.1 Gastric Lavage Procedure

The gastric lavage performed in this study followed the procedure as described by Elston *et al.* (2015). The shark was held ventral side up to induce tonic immobility and a clear, flexible plastic tube with an outer diameter of 20 mm and beveled edges was inserted through the mouth and into the stomach. Saltwater was pumped from a bucket into the stomach using an electronic, submersible bilge pump (31.5 L/min). The individual's body was angled downwards to capture the stomach contents in a mesh sampling bag. This procedure was repeated until no stomach contents were observed exiting the stomach. Afterwards, the tube was removed, the shark brought out of tonic immobility and released at the site of capture. The stomach content was transferred to a ziplock bag, stored in a freezer (-8°C) and frozen until ready to be analysed.

2.3.2 Tagging Procedure

Individuals were caught in Mossel Bay from land and at sea at three sites: Roman's Reef, Mitch Reef, and Darwin Reef. Tonic immobility was not suitable to subdue the species, as the surgical incision forced the animal out of tonic immobility and to become agitated. Therefore captured animals were brought under anaesthesia using 2-phenoxyethanol in a concentration of 0.7 and 1 ml/L seawater (for *P. pantherinum* and *P. africanum*, respectively). Concentration was derived from Escobar-Porras (2009). Once the individual was under partial to complete anaesthesia (A3 to A4; Keene *et al.*, 1998), they were turned ventral-side up and prepared for surgery, ensuring the mouth and gills were submerged in water, while the belly was exposed for surgery. A surgical incision, approximately 2 cm in length, was made on the ventral side, approximately halfway to two-thirds down between the pectoral and pelvic fins, and the acoustic transmitter inserted. The transmitter was an Innovasea V16-4H transmitter, operating at a 69 kHz frequency, a 90-second nominal delay and with an expected battery life of 1013 days. Three stitches were used to close the incision, and wound powder, an antiseptic powder that gelifies in contact with water, was added to the surgical area to add an extra layer of protection. The animal was placed back in the tub of seawater to recover in an upright position. Once the animal was fully recovered, considered to be responsive to stimuli and capable of movement on its own, it was released at the site of capture.

Chapter 3

Ichthyofaunal Reef Assemblage of Mossel Bay and Temporal Variation in Abundance of *Poroderma* spp.

3.1 Introduction

Community ecology involves the explanation of patterns in the distribution, abundance and interaction of species (Leibold *et al.*, 2004). The community of an area is described as all the individuals of all species that interact within a locality (Leibold *et al.*, 2004), whereby a community can be either open, experiencing some form of migration into or out of the locality, or closed (Leibold *et al.*, 2004). An ecological community is composed of various factors, including predators, herbivores, flora, decomposers, and pathogens, while a trophic web in turn is composed primarily of predators, herbivores, and their flora (Vellend, 2016).

The complexity of ecological communities, and fluctuations in resource availability, can in the long run result in interactions such as predation, competition, mutualism, and others (Vellend, 2016; Krebs, 2014). Competition in turn can result in resource (competing for limited resources) or interference (harming another organism despite abundant resources) competition (Krebs,

2014). If two coexisting species competing for the same resources have different fitnesses, and there is no possibility of niche differentiation, one species might outcompete the other (Chesson, 2000).

Within the marine community chondrichthyans play a the crucial role in their ecosystem (as apex and mesopredators). Gaining an understanding of the impact of these species on their community is essential to predict how these communities might react as a result of changes due to anthropogenic or climatic sources. When resources are abundant, sympatric mesopredators can coexist, as seen in small elasmobranchs around Maryland, which showed a high degree of overlap in diet composition, spatial distribution, and diel stomach fullness (Woodland *et al.*, 2011). However, if prey shared by these predators were to become scarce, competitive interactions would be possible (Woodland *et al.*, 2011). An assemblage of morphologically similar, sympatric predators can therefore be expected to exhibit fine-scale habitat segregation, or resource partitioning, to reduce the effects of direct competition (Humphries *et al.*, 2016).

Poroderma africanum and *Poroderma pantherinum* are two sympatric, mesopredatory Scyliorhinidae, endemic to southern Africa. Both species have similar distribution ranges, and are thought to prey on similar species (Ebert *et al.*, 2021a). They are known to occur together on inshore rocky reefs despite seemingly occupying similar ecological niches (Ebert *et al.*, 2021a). Variation in abundance of competing predators has shown to allow for coexistence within the same area (Sabando *et al.*, 2020), however, this has not been previously explored within sympatric, South African elasmobranchs. Apart from inter-specific abundance variation, understanding how the two species co-occur within the reef fish community structure of Mossel Bay provides a valuable information on the ecological role these two species perform here.

While both *Poroderma* spp. have been repeatedly sighted in various BRUV studies around South Africa (e.g., Bernard and Götz, 2012; de Vos *et al.*, 2015; Roberson *et al.*, 2015), no study has looked at these two species in-depth comparatively or over a multi-year period. While a seasonal component was part of de Vos *et al.* (2015), this was not further explored over a multi-year period.

This chapter aimed to examine the ichthyofaunal assemblage of three reefs along the western side of Mossel Bay using BRUVs, with particular attention to how the study species *P. africanum* and *P. pantherinum* are represented, and examine how these two species co-exist across temporal scales. The primary research questions of this chapter were as follows:

- What is the composition of the ichthyofaunal assemblage along the reefs of Mossel Bay, and how are the *P. africanum* and *P. pantherinum* species represented within that?
- Is there temporal variation in abundance of *P. africanum* and *P. pantherinum*?
- What are the environmental relationships for the ichthyofaunal diversity within Mossel Bay?

3.2 Methods

3.2.1 Field Deployment

The BRUV rig, as described in Section 2.2.1, was deployed from a vessel on the three target reefs: Roman's Reef, Mitch Reef and Darwin Reef (Figure 3.1), between August 2015 and March 2018. As the three target reefs were geologically similar, composed of Table Mountain Group sandstone (Cawthra, 2014), and had similar reef profiles, habitat structure was not considered a parameter in any statistical analysis. A small reef (Santos Reef, indicated in purple; Figure 3.1) located just south of Mitch Reef was considered to be part of Mitch Reef for this study, due

to its proximity (± 100 m), similar depth, reef profile, and sessile fauna and flora. BRUV deployments were performed across the full extend of the reefs' depth.

To evenly spread the BRUV deployments across the year, deployments were grouped into yearly quarters (January to March, April to June, etc.), which in turn were grouped into seasons (Summer: October to March; Winter: April to September) to allow for comparison across other studies (de Vos *et al.*, 2014). At the site of deployment, the bait canister was filled with approximately 500 gr chopped *Sardinops sagax* (sardines). The camera was switched on and the rig lowered to the seafloor. Subsequently, the vessel moved away from the deployment area (>200 m), to ensure no interference from the presence of the vessel occurred. The deployment lasted for 60 minutes (de Vos *et al.*, 2014; Currey-Randall *et al.*, 2020) before the rig was picked up and the camera switched off. Once returned to shore, the videos were downloaded and analysed.

3.2.2 Abiotic Data

At each deployment site a number of positional and environmental parameters were recorded. Latitude, longitude and time of deployment were recorded from the vessel's on-board computer. Depth (m) was determined from the boat's eco-sounder, while swell height (m) and cloud cover (percentage overhead coverage) was estimated at the time of each deployment. Daily satellite sea surface temperature (SST, °C) was obtained via NOAA's online dataset (`https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST.html`, collected on the 22nd of June 2018). Barometric pressure (hPa), rainfall (mm), wind speed (m/s) and direction were provided by the South African Weather Service (SAWS) for Mossel Bay. These parameters were included in the analyses as they have been suggested to influence the behaviour of fish species (Peterson, 1972; Guy *et al.*, 1992; Heupel *et al.*, 2003; Stoner, 2004). Tidal data were provided by the South African Navy Hydrographer Office for Mossel Bay, while lunar phase

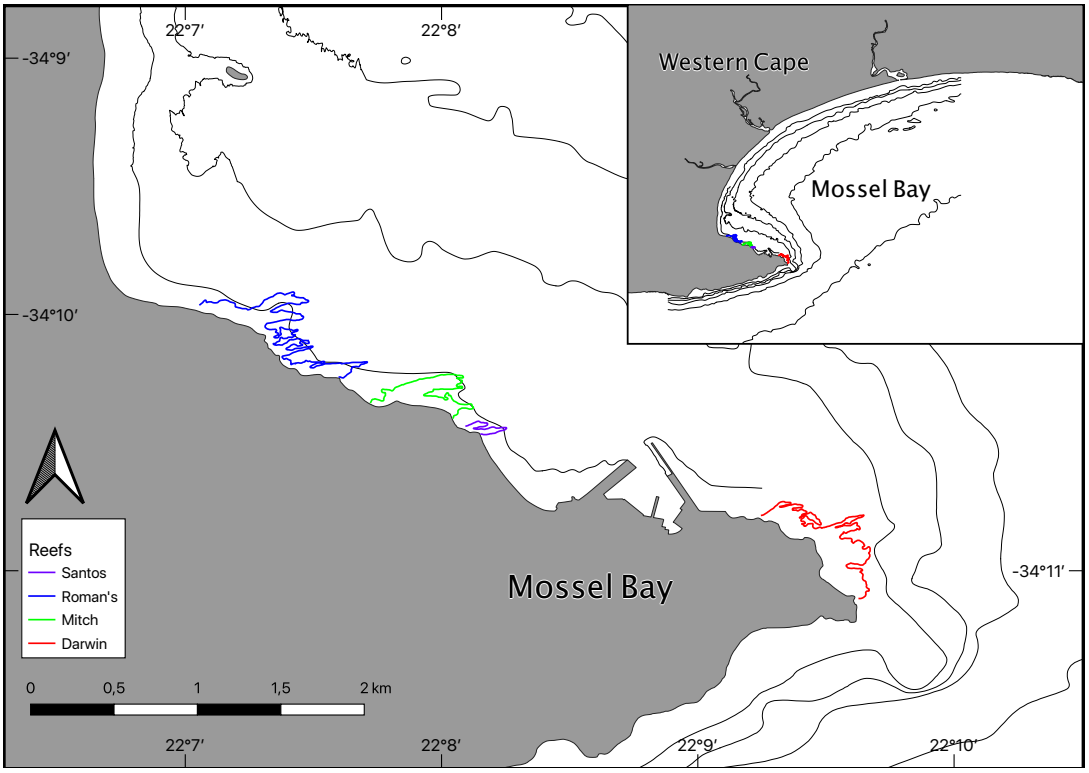


Figure 3.1: Location of the target reefs in the Mossel Bay area with positions of BRUV deployments. The outlines of the reefs are coloured independently. A small separate reef, Santos Reef (purple), was considered part of Mitch Reef (green) for this study due to its proximity and overall similarity. Inset map: Whole of the Mossel Bay area. Created with qGIS v3.12.

(described as a percentage of lunar illumination) data were collected from the website `www.vercalendario.info`.

3.2.3 Video Analysis

All videos were analysed using VLC (Version 2.2.1), which allowed for adjustments of colour balance and image transformation for better identification of species that were difficult to identify. For each deployment, habitat was confirmed as consolidated reef, and every teleost, chondrichthyan and large free-swimming species were identified and the time the first individual of a species arrived was recorded as T1st, in minutes:seconds. T1st can be used to infer the distance an individual travels to the BRUV. However, this is also influenced by the behaviour

of the species towards the bait (Whitmarsh *et al.*, 2017), and their response to the activity around the bait canister (Cappo *et al.*, 2007).

The MaxN was used as a measure for abundance, defined as the maximum number of individuals of a species seen within a frame throughout the entire 60-minute deployment (de Vos *et al.*, 2015). MaxN is a conservative measure for Relative Abundance (RA), as more individuals of a species may be present around the rig, but would not be counted as they would not appear within the Field-of-View. However, MaxN avoids pseudo-replication as a result of individuals swimming in and out of the Field-of-View (Willis *et al.*, 2003). A downside occurs when too many individuals of a species appear within the Field-of-View, resulting in saturation (Schobernd *et al.*, 2014; Stobart *et al.*, 2015). It would be problematic to detect differences between localities as a result of saturation, and the MaxN would be non-linearly related to the true abundance of a species (Whitmarsh *et al.*, 2017). MaxN was recorded manually, and the time this occurred was recorded as Time of MaxN (in minutes:seconds). A negative correlation has been found between T1st and MaxN, indicating that when a species arrives quickly within the field of view, there is a strong possibility it is highly abundant (Stobart *et al.*, 2015).

3.2.4 Statistical Analyses

The individual species were described by %Frequency of Occurrence, Relative Abundance (RA) and minimum and maximum MaxN values. The %Frequency of Occurrence was calculated as the number of deployments the species was seen on, divided by the total number of deployments; the RA of each species was calculated as the sum of MaxN, divided by the total number of deployments (Equation 3.2.1; de Vos *et al.*, 2014). Shannon-Wiener (Equation 3.2.2; Ludwig and Reynolds, 1988) indices were calculated for each sample, which used the MaxN value as a proxy for abundance.

$$RA_i = \frac{\sum \texttt{MaxN}_i}{\sum \texttt{Deployment}} \quad \text{(eq. 3.2.1)}$$

$$H' = \sum_{i=1}^{s} (p_i \; ln \; p_i) \quad \text{(eq. 3.2.2)}$$

In the Shannon index (Equation 3.2.2), p_i is the proportion (n_i/N) of individuals of one species (n_i) divided by the total number of individuals found (N), and s is the total number of species (Ludwig and Reynolds, 1988). An ANOVA was used to compare the diversity between reefs and quarters, while a Student's t-test was used to compare between summer and winter. If the ANOVA results were significant, a Tukey-HSD post-hoc test was performed to identify which grouping caused the significance.

All data utilized for parametric analyses were tested using Shapiro-Wilk tests for normality using R's `shapiro.test` function, and non-parametric tests were utilized if the data were not normally distributed (i.e. Wilcoxon Sum Rank tests and Kruskal-Wallis test). All the statistical analyses were performed using R v3.5.2 (R Core Team, 2019).

3.2.4.1 Rarefaction Curve

To examine the relation between effort and result, a rarefaction curve was constructed (Sanders, 1968; Chiarucci *et al.*, 2008). To exclude sampling order bias, the rarefaction analysis randomizes the order in which the stomachs were analysed 100 times (Gotelli and Colwell, 2001). When the curve reaches an asymptote it is assumed that the full extent of the ichthyofaunal assemblage has been reached (or as close as the method allows). However, in natural open ecosystems, reaching an actual asymptote is rarely reached due to the detection or identification of vagrant and rare species (Gotelli and Colwell, 2011). The rarefaction curve was constructed using the `specaccum` function (with

method="rarefaction") from vegan package in R (Oksanen *et al.*, 2013).

A linear regression was conducted on the mean cumulative number of species in the final three samples to quantitatively determine if the slopes reached an asymptote (Bizzarro *et al.*, 2007). The slope of the linear regression was statistically compared to a slope of 0 using a Student's t-test:

$$t = \frac{b - 0}{S_b} \qquad \text{(eq. 3.2.3)}$$

where b is the slope of the linear regression and S_b is the standard error of the slope (Bizzarro *et al.*, 2007).

A bootstrap estimation was performed using the specpool function from the vegan package (Oksanen *et al.*, 2013) to extrapolate the species richness based on the sample pool, and determine the estimated percentage of species the BRUV deployments have identified.

3.2.4.2 Community Structure

The community structure of the ichthyofaunal biodiversity was analysed using a non-metric Multi-Dimensional Scaling (nMDS) plot, followed by a PERMANOVA. Any significant result from the PERMANOVA was further examined using a SIMPER analysis.

The dissimilarities of BRUV deployments between the different reef sites were compared through a nMDS plot, based on a Bray-Curtis dissimilarity matrix. To down-weight the influence of overabundant species, the MaxN values were fourth-root transformed. The nMDS plot was constructed using the metaMDS function of the vegan package across 3 dimensions ($k = 3$), with distance specified as "bray" (Oksanen *et al.*, 2013). Specific environmental parameters (depth, SST, swell height, tide, barometric pressure, wind speed and direction and lunar phase) potentially driving the dissimilarity among the different deployments were overlaid onto the nMDS plot using vegan's envfit-function. An ANOSIM analysis (Clarke

and Green, 1988) was performed on the Bray-Curtis dissimilarity matrix using the `anosim` function of the `vegan` package (Oksanen *et al.*, 2013) to compare the similarities of the BRUV deployments across the different reef sites.

A PERMANOVA analysis (Anderson, 2001) was performed on the fourth-root transformed MaxN data to determine whether the different reef sites, seasons, quarters or years elicited differences on the species composition. The analysis was performed using the `adonis2` function of the `vegan` package (Oksanen *et al.*, 2013).

Similarity Percentage (SIMPER) analyses (Clarke, 1993) were performed on the factors that contributed significant differences to the species composition determined by the PERMANOVA analysis. The SIMPER analyses would identify which species contributed towards these differences. The analyses were performed using the `simper` function of the `vegan` package (Oksanen *et al.*, 2013).

3.2.4.3 Presence/Absence

Binomial generalized linear models were created to compare the presence and absence of *P. africanum* and *P. pantherinum* against the most influential environmental parameters indicated by the nMDS plot: SST, barometric pressure, depth, tide, lunar phase, and wind direction and speed. All parameters were examined additively, while tide and lunar phase were considered correlated. All combinations of these environmental variables were examined against the species' presence and absence using `MuMIn`'s `dredge`-function (Barton and Barton, 2015; Appendix B). Akaike Information Criterion (AIC) (Akaike, 1973) was used to determine the best fitting model, which was then further examined.

3.2.4.4 Co-occurrence

A probabilistic co-occurrence model was created (Veech, 2013) to determine the co-occurrence probability of the various species, with particular focus on the two study

species, seen during the BRUV deployments. A probabilistic model was chosen as it reduces the chances of Type I and Type II errors and is not reliant on any data transformation as compared with randomisation tests (Veech, 2013). Positive co-occurrence would signify that two species occur together at more locations than would be expected if each were randomly distributed relative to the other species, while a negative co-occurrence would signify that two species occur together at fewer locations than would be expected (Veech, 2013).

An association network based on the non-random co-occurrences was generated using `igraph` package in R (Csardi and Nepusz, 2006). The network was visualized using an MDS strain-model layout algorithm (Hu, 2011). To determine the gregarious nature of species in relation to non-random, co-occurring species, Eigenvector Centrality was calculated using `igraph`'s `eigen_centrality`-function (Csardi and Nepusz, 2006), weighted according to the pair-wise positive and negative association derived from the co-occurrence analysis (Farine and Whitehead, 2015).

3.3 Results

3.3.1 Abiotic Description

Between August 2015 and April 2018, SST in Mossel Bay ranged from 13.9 °C to 24.5 °C, with a yearly average of 18.2 °C ± 2.35 °C (Figure 3.2) (mean ± sd). SST on days of BRUV deployments ranged from 14.2 °C to 23.2 °C. The wind direction in Mossel Bay was dominated by an east-west axis, with the wind coming predominantly from the west. Wind speed ranged from 0 to 45 km/h (24.3 knots).

The BRUVs were deployed over a depth range of 2.4 m to 10.4 m, with an average depth of 5.2 m ± 1.2 m (mean ± sd) at Roman's Reef, 4.5 m ± 1.2 m at Mitch Reef, and 5.7 m ± 1.3 m at Darwin Reef.

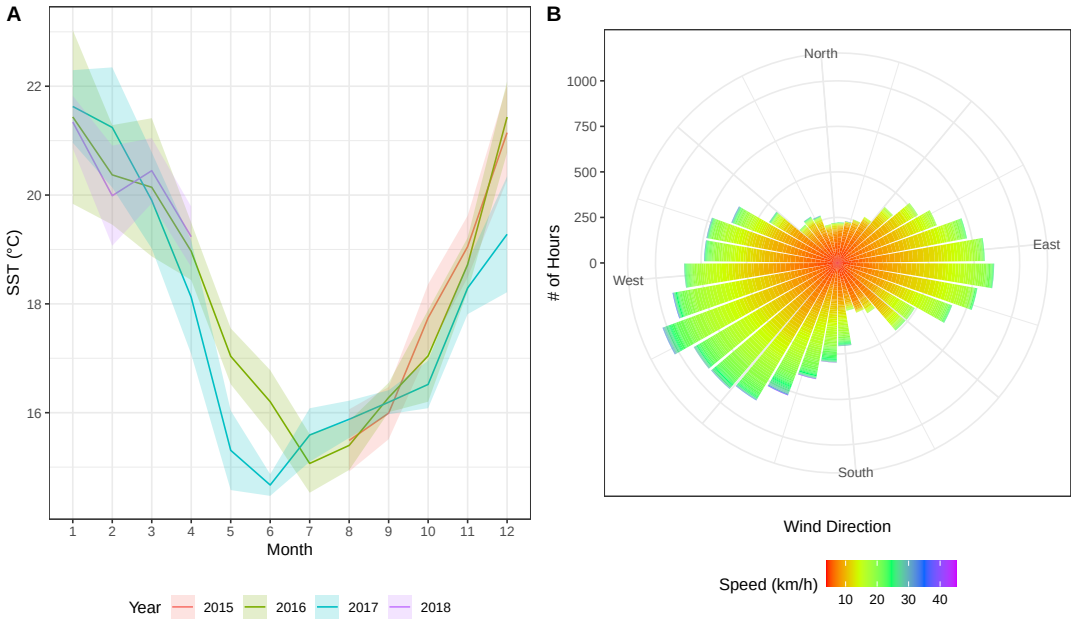


Figure 3.2: (A) Monthly mean (± sd) Sea Surface Temperature (in °C) and (B) predominant wind direction and speed in Mossel Bay, South Africa between August 2015 and March 2018.

3.3.2 Diversity

A total of 197 BRUV deployments were analysed, deployed relatively equally across the three reefs (Roman's Reef: n = 65; Mitch Reef: n = 64; Darwin Reef: n = 68) between August 2015 and March 2018. Approximately eight BRUV rigs were deployed per reef per quarter.

The analysis of the deployments resulted in the identification of 65 species, of which three were only identifiable down to the taxonomic level of Class (i.e unidentified Chondrichthyan or Osteichthyan), and four down to family or genus level (Table 3.1). These species were removed from further analysis due to uncertainty. A total of 10 chondrichthyan species, 42 osteichthyan species, and 6 non-fish species were identified to species level.

The study species, *P. africanum* and *P. pantherinum*, were seen in 39.1% and 17.3% of the deployments respectively, and were the second and third most abundant chondrichthyan species found during this study (RA = 0.52 and 0.2,

respectively). *Haploblepharus edwardsii* (puffadder shyshark) was the most abundant chondrichthyan species (RA = 0.64), seen in 55.3% of the deployments (Table 3.1). The ichthyofauna was dominated by seabream (Sparidae), with eight out of the nine osteichthyan with the highest RA all belonging to this family. The most abundant non-fish species was *Octopus vulgaris* (common octopus) with RA = 0.442, seen in 39.1% of the deployments.

The mean species diversity of all the deployments using the Shannon-Wiener diversity index was 1.53 ± 0.31 (mean ± sd), with a range of 0.84 to 2.4. While the species diversity was not significantly different amongst the three target reefs ($F = 0.602$, $p = 0.549$), the species diversity was significantly different between summer and winter ($t = 4.306$, $p < 0.001$), and by quarters ($F = 10.568$, $p < 0.001$). The first quarter (January – March) was significantly different from all other quarters (Figure 3.3). Darwin Reef showed a larger number of unique identified species compared with Mitch and Roman's Reef. Darwin Reef showed 10 unique species, comprised of seven actinopterygii, two aves, one mammalia; Mitch Reef showed three unique species: two actinopterygii and one scyphozoa; and Roman's Reef showed five unique species: three actinopterygii and two chondrichthyes.

3.3.3 Rarefaction Curve

Following the construction of the rarefaction curve (Figure 3.4), the final slope of the curve for the whole study site was calculated at 0.056. A quantitative exploration of the curve through the use of a Student's t-test showed that the end slope of the rarefaction curve was significantly different from a 0-slope ($t = 936.85$, $p < 0.001$). While this indicated that the description of the biodiversity on the Mossel Bay reefs through BRUVs was not yet reached, a bootstrap estimation indicated that the maximum richness of the Mossel Bay reefs is approximately 63.4 (± 1.9, SE) species. Thus the BRUV deployments identified an estimated 91.5% of species on the reefs of Mossel Bay. Examination of the individual reefs showed that the

Table 3.1: Table with the class, family and latin name of species sighted on the BRUV deployments in Mossel Bay, with % Frequency of Occurrence, Relative Abundance (RA), and the minimum and maximum MaxN values, ordered by descending RA. The study species *P. africanum* and *P. pantherinum* are highlighted in bold.

Class	Family	Latin Name	Frequency of Occurrence (%)	RA	MaxN Min	MaxN Max
Osteichthyes	Sparidae	*Sarpa salpa*	81.7	24.772	1	195
Osteichthyes	Sparidae	*Spondyliosoma emarginatum*	91.4	14.376	1	80
Osteichthyes	Sparidae	*Diplodus capensis*	97.5	11.107	1	58
Osteichthyes	Sparidae	*Boopsoidea inornata*	71.1	9.056	1	75
Osteichthyes	Haemulidae	*Pomadasys olivaceum*	51.8	6.675	1	74
Osteichthyes	Sparidae	*Chrysoblephus laticeps*	97	3.274	1	7
Osteichthyes	Sparidae	*Lithognathus mormyrus*	57.9	1.629	1	27
Osteichthyes	Sparidae	*Diplodus hottentotus*	58.4	0.761	1	5
Osteichthyes	Sparidae	*Cheimerius nufar*	43.1	0.665	1	7
Osteichthyes	Latridae	*Chirodactylus brachydactylus*	44.7	0.665	1	9
Chondrichthyes	Scyliorhinidae	*Haploblepharus edwardsii*	55.3	0.64	1	2
Osteichthyes	Mugilidae	*Liza richardsonii*	1	0.523	2	101
Chondrichthyes	**Scyliorhinidae**	***Poroderma africanum***	**39.1**	**0.518**	**1**	**5**
Cephalopoda	Octopodidae	*Octopus vulgaris*	39.1	0.442	1	3
Osteichthyes	Sparidae	*Argyrozona argyrozona*	12.2	0.365	1	28
Osteichthyes	Carangidae	*Trachurus trachurus*	1	0.36	25	46
Osteichthyes	Tetraodontidae	*Amblyrhynchotes honckenii*	28.9	0.335	1	4
Osteichthyes	Clinidae	*Clinus superciliosus*	28.9	0.305	1	2
Osteichthyes	Scombridae	*Scomber japonicus*	2	0.264	3	24
Osteichthyes	Chaetodontidae	*Chaetodon marleyi*	20.3	0.244	1	3
Chondrichthyes	**Scyliorhinidae**	***Poroderma pantherinum***	**17.3**	**0.198**	**1**	**2**
Osteichthyes	Epinephelidae	*Epinephelus marginatus*	13.2	0.173	1	5
Osteichthyes	Sparidae	*Lithognathus lithognathus*	9.6	0.168	1	7
Osteichthyes	Sparidae	*Gymnocrotaphus curvidens*	13.2	0.152	1	2
Osteichthyes	Pomatomidae	*Pomatomus saltatrix*	7.6	0.152	1	10
Osteichthyes	Cheilodactylidae	*Cheilodactylus fasciatus*	11.2	0.117	1	2
Osteichthyes	Oplegnathidae	*Oplegnathus conwayi*	8.6	0.102	1	3
Osteichthyes	Mullidae	*Parupeneus rubescens*	5.6	0.096	1	4
Mammalia	Otariidae	*Arctocephalus pusillus pusillus*	7.6	0.086	1	2
Osteichthyes	Ariidae	*Galeichthys feliceps*	7.1	0.076	1	2
Chondrichthyes	Dasyatidae	*Bathytoshia brevicaudata*	7.1	0.071	1	1
Osteichthyes	Sparidae	*Rhabdosargus holubi*	4.6	0.061	1	2
Chondrichthyes	Myliobatidae	*Aetomylaeus bovinus*	4.6	0.056	1	2
Chondrichthyes	Triakidae	*Mustelus mustelus*	5.6	0.056	1	1
Osteichthyes	Dichistiidae	*Dichistius capensis*	4.6	0.046	1	1
Osteichthyes	Sparidae	*Rhabdosargus globiceps*	3.6	0.046	1	3
Chondrichthyes	Odontaspididae	*Carcharias taurus*	3	0.03	1	1
Osteichthyes	Carangidae	*Lichia amia*	2	0.03	1	2
Osteichthyes	Epinephelidae	*Epinephelus andersoni*	2.5	0.025	1	1
Osteichthyes	Blenniidae	*Scartella emarginata*	2.5	0.025	1	1
Chondrichthyes	Myliobatidae	*Myliobatis aquila*	1.5	0.02	1	2
Osteichthyes	Clinidae	*Pavoclinus graminis*	1.5	0.02	1	2
Aves	Phalacrocoracidae	*Phalacrocorax spp.*	2	0.02	1	1
Osteichthyes	Clinidae	*Clinidae spp.*	1.5	0.015	1	1
Osteichthyes	Echeneidae	*Echeneis naucratus*	1	0.015	1	2
Chondrichthyes	Lamnidae	*Carcharodon carcharias*	1	0.01	1	1
Osteichthyes	Muraenidae	*Muraenidae spp.*	0.5	0.01	2	2
Osteichthyes	Sparidae	*Pachymetopon grande*	1	0.01	1	1
Osteichthyes	Sparidae	*Sparodon durbanensis*	1	0.01	1	1
Chondrichthyes	Rhinobatidae	*Acroteriobatus annulatus*	0.5	0.005	1	1
Osteichthyes	Cheilodactylidae	*Cheilodactylus pixi*	0.5	0.005	1	1
Osteichthyes	Mugilidae	*Chelon dumerili*	0.5	0.005	1	1
Chondrichthyes		*Chondrichthyan spp.*	0.5	0.005	1	1
Osteichthyes	Clinidae	*Clinus spp.*	0.5	0.005	1	1
Scyphozoa	Rhizostomatidae	*Eupilema inexpectata*	0.5	0.005	1	1
Osteichthyes	Mugilidae	*Mugil cephalus*	0.5	0.005	1	1
Osteichthyes		*Osteichthyan spp. 1*	0.5	0.005	1	1
Osteichthyes		*Osteichthyan spp. 2*	0.5	0.005	1	1
Osteichthyes	Sparidae	*Pachymetopon aeneum*	0.5	0.005	1	1
Aves	Phalacrocoracidae	*Phalacrocorax lucidus*	0.5	0.005	1	1
Chondrichthyes	Scyliorhinidae	*Scyliorhinidae spp.*	0.5	0.005	1	1
Osteichthyes	Carangidae	*Seriola lalandi*	0.5	0.005	1	1
Aves	Spheniscidae	*Spheniscus demersus*	0.5	0.005	1	1
Mammalia	Delphinidae	*Tursiops aduncus*	0.5	0.005	1	1
Osteichthyes	Sciaenidae	*Umbrina robinsoni*	0.5	0.005	1	1

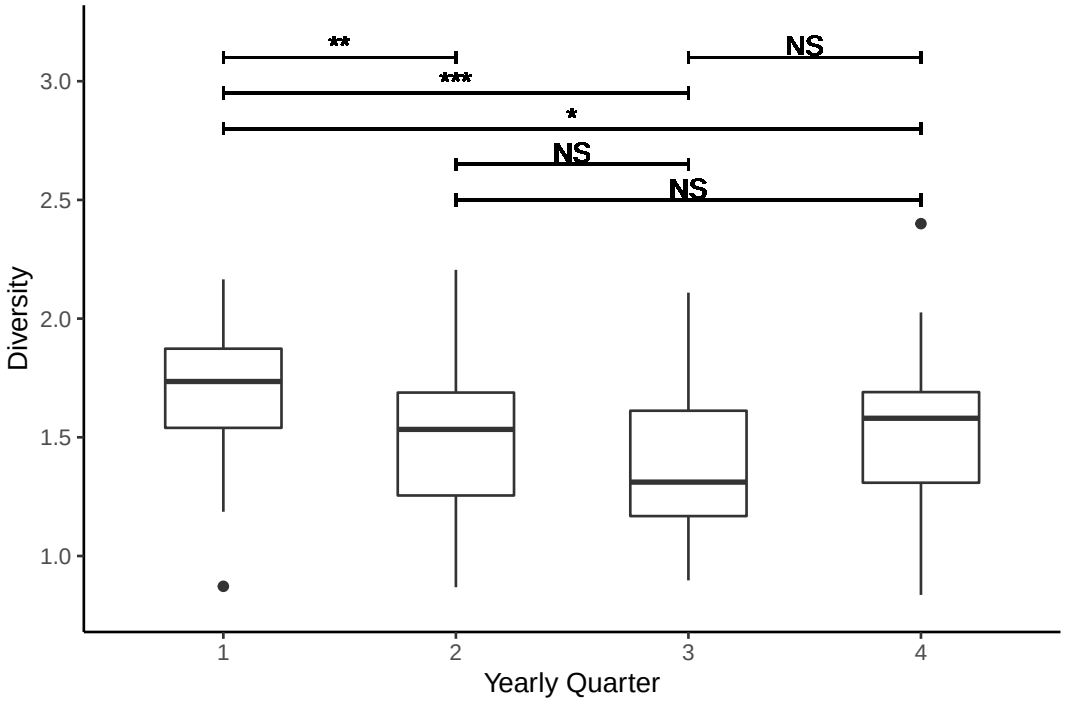


Figure 3.3: Tukey-HSD result of BRUV diversity amongst the four annual quarters. Quarter 1 = January to March, Quarter 2 = April to June, Quarter 3 = July to September, Quarter 4 = October to December

maximum richness had not yet been reached (Roman's Reef slope = 0.140; Mitch Reef slope = 0.141; and Darwin Reef slope = 0.133).

3.3.4 Community Structure

A nMDS plot using three dimensions ($k = 3$) was constructed to examine the similarities in fish community structure amongst the three reef sites in Mossel Bay, and to investigate the role of selected environmental variables (SST, barometric pressure, tide, depth, wind speed and direction, swell and lunar phase) (Figure 3.5). The nMDS plot has a stress level of 0.184, indicating that the plot was a good fit.

Fish species composition at Mitch and Roman's Reef were similar, with the 95% ellipses overlapping nearly perfectly across all three dimensions (Figure 3.5). Darwin Reef showed a partial overlap with Mitch/Roman's Reef deployments along

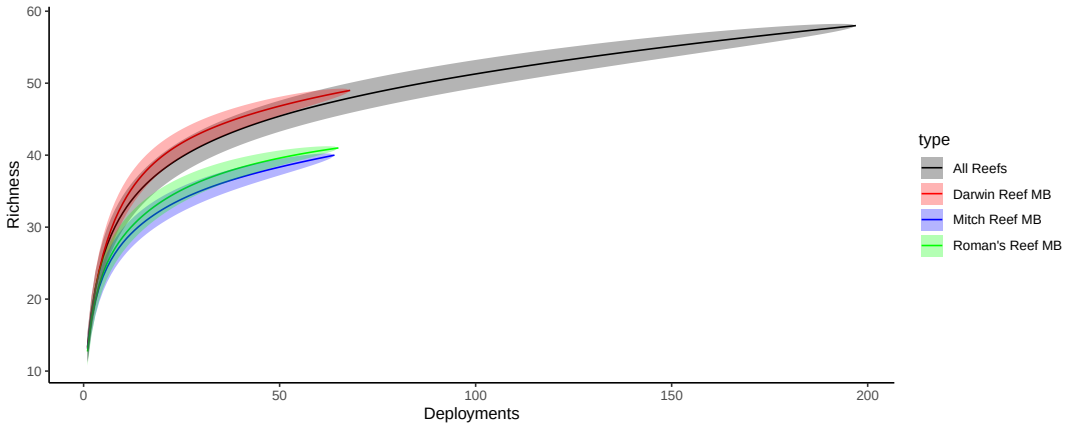


Figure 3.4: Species accumulation curves of Roman's, Mitch and Darwin Reef, and the three reefs combined. The shaded areas indicate the standard deviation around the mean number of cumulative species for the number of BRUV deployments analysed after 100 randomisations.

two dimensions, which indicates that the fish species composition between Darwin Reef and Mitch/Roman's Reef, while partially overlapping, was different. This was confirmed with the ANOSIM which showed that the significant difference in the species composition of the BRUV deployments amongst the reef sites ($R = 0.165$, $p = 0.001$) was driven by Darwin Reef, where Roman's and Mitch Reef showed similar dissimilarity ranks within their reefs (Figure 3.6). Identifiable species vectors showed that the two avian species *Spheniscus demersus* (African penguin) and *Phalacrocorax lucidus* (white-breasted cormorant), and marine species *Cheilodactylus pixi* (barred fingerfin), *Sparodon durbanensis* (white musselcracker), *C. carcharias*, *Umbrina robinsoni* (slender baardman), *Mugil cephalus* (flathead mullet) and *Acroteriobatus annulatus* (lesser guitarfish) were strong species indicators of the variability among the three reef sites (Figure 3.5A and C). This is also supported by Darwin Reef having a higher number of unique identifiable species compared with Mitch and Roman's Reef (10 unique species at Darwin Reef, compared with three and five at Mitch and Roman's Reef, respectively).

Fitting the environmental parameters over the nMDS plot showed that wind, swell and lunar phase had little influence over the fish-community structure of the

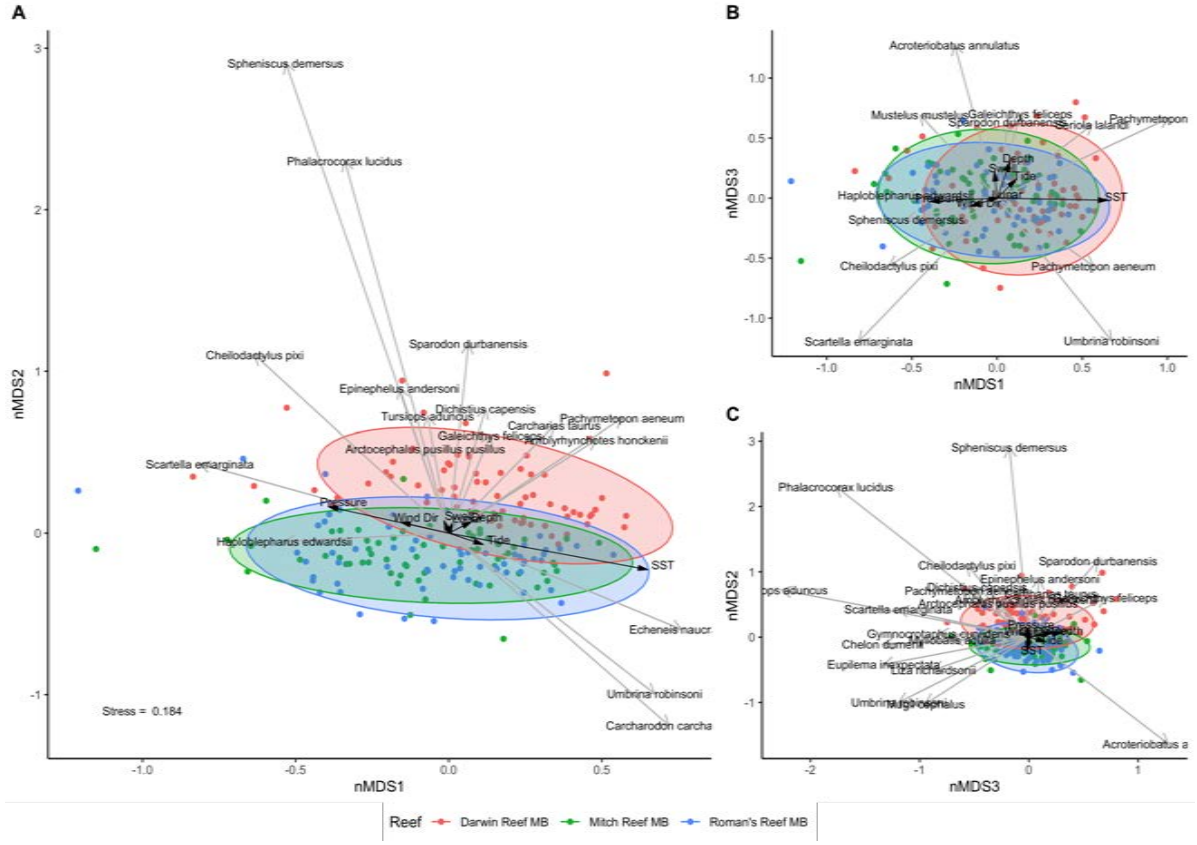


Figure 3.5: Non-metric Multi-Dimensional Scaling plots of BRUV deployments based on species-compositions and MaxN across 3 dimensions, with selected environmental parameters and predominant species fitted. (A) a plot visualizing the x and y-axes; (B) visualizing the x and z-axes; and (C) visualizing the y and z-axes. Only species with a vector longer than 0.5 along the x and y-axis were visualized to avoid overcrowding of non-informative species vectors.

reefs. SST and barometric pressure were shown to strongly correlated to the fish-community structure both within locations (Figure 3.5A) and between locations (Figure 3.5B). Depth had a weak influence on the variation in fish-community structure between locations (Figure 3.5C).

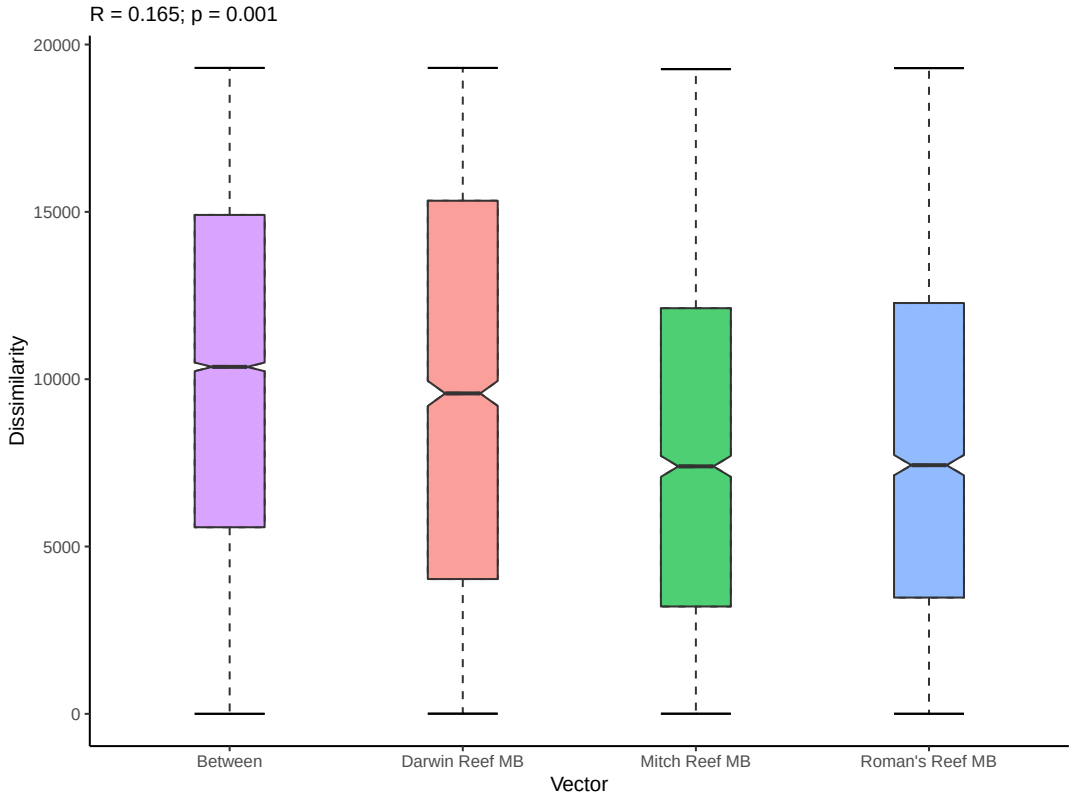


Figure 3.6: Boxplot of ANOSIM results on the fish assemblage of the BRUV deployments across the different reefs with ANOSIM R-statistic and p-value.

The results of the PERMANOVA analysis on the fourth-root transformed MaxN data indicated that differences in community structure were elicited by differences between the reef sites ($F = 14.38$, $p < 0.001$), summer and winter ($F = 21.14$, $p < 0.001$), the different quarters ($F = 6.23$, $p < 0.001$), and years ($F = 3.23$, $p < 0.001$; Table 3.2). A combination of reef sites and quarters were also eliciting differences in community structure ($F = 1.76$, $p < 0.05$), but not a combination of reefs and seasons ($F = 1.55$, $p = 0.08$), or reefs and years ($F = 0.87$, $p = 0.733$).

Table 3.2: Results of the PERMANOVA performed on the population composition of the BRUV deployments. Independent variables included reef site, season, quarter and year.

	Df	**SumOfSqs**	**R2**	**F**	**Pr(>F)**
Reef	2.00	2.43	0.11	14.38	0.00
Season	1.00	1.79	0.08	21.14	0.00
Quarter	2.00	1.05	0.05	6.23	0.00
Year	3.00	0.82	0.04	3.23	0.00
Reef:Season	2.00	0.26	0.01	1.55	0.08
Reef:Quarter	4.00	0.60	0.03	1.76	0.01
Reef:Year	6.00	0.44	0.02	0.87	0.73
Residual	176.00	14.89	0.67		
Total	196.00	22.28	1.00		

A subsequent SIMPER analysis indicated that between 16 and 17 species contributed cumulatively over 75% to the differences between the different reef sites (16 species between Darwin Reef and Mitch Reef, and Mitch and Roman's Reef; 17 species between Darwin and Roman's Reef) (Tables A.2 and A.3). When examining the species contributions between seasons, a SIMPER analysis indicated that 16 species cumulatively contributed to 76.4% to the differences between summer and winter, with the top three species (*Sarpa salpa* (strepie), *Boopsoidea inornata* (fransmadam), and *P. olivaceum* (olive grunter)) contributing 25.7% to the differences in species composition between the two seasons (Table A.4). The same analysis, but examining the different quarters, revealed that 16 species cumulatively contributed over 75% to the differences between these (Tables A.6 to A.10). Lastly, looking at the contribution of species to the variation between years, the SIMPER analysis indicated that between 14 and 16 species cumulatively contributed over 75% to the differences between these (14 species between 2015 and 2017; 15 species between 2015 and 2016, and 2015 and 2018; and 16 species

between 2016 and 2017, 2016 and 2018, and 2017 and 2018). The top five of the species contributing to the differences in species composition between the years were present in all years (Tables A.11 to A.16).

3.3.5 Species Analysis

The RA between the two *Poroderma* spp. (Table 3.3) were significantly different, with *P. africanum* showing overall a higher RA value than *P. pantherinum* ($W = 23737$, $p < 0.001$); however, within the species between the reef sites there was no significant variation in RA (*P. africanum*: $\chi^2 = 0.016$, $p = 0.992$; *P. pantherinum*: $\chi^2 = 0.011$, $p = 0.994$). *Poroderma africanum* and *P. pantherinum* appeared in the BRUV deployments on average around the same time, at 23 min 37 sec ± 16 min 35 sec (mean ± sd) and 21 min 56 sec ± 16 min 1 sec, respectively ($t = 0.64$, $p = 0.524$, Figure 3.7A), and reached their MaxN around the same time, at 26 min 8 sec ± 16 min 46 sec (mean ± sd) and 23 min 1 sec ± 15 min 4 sec, respectively ($t = 0.354$, $p = 0.725$, Figure 3.7B).

A significant difference in MaxN values between summer and winter was found for *P. africanum* ($W = 3806$, $p < 0.01$), but not for *P. pantherinum* ($W = 4354$, $p = 0.059$). The RA calculated per quarter was on average significantly higher for *P. africanum* than for *P. pantherinum* ($W = 9.5$, $p < 0.001$).

Table 3.4: Tukey-HSD results of the adjusted quarterly RA values of *P. africanum*.

	diff	**lwr**	**upr**	**p adj**
2-1	0.27	-0.16	0.69	0.24
3-1	0.79	0.36	1.22	0.00
4-1	-0.02	-0.40	0.36	1.00
3-2	0.52	0.06	0.99	0.03
4-2	-0.29	-0.71	0.14	0.19
4-3	-0.81	-1.24	-0.39	0.00

Poroderma africanum was more abundant during the winter months, with RA values of 0.665 and 0.860 in quarters 2 and 3, respectively, compared with 0.401 and 0.377 in quarters 1 and 4, respectively (Figure 3.8). However, the differences

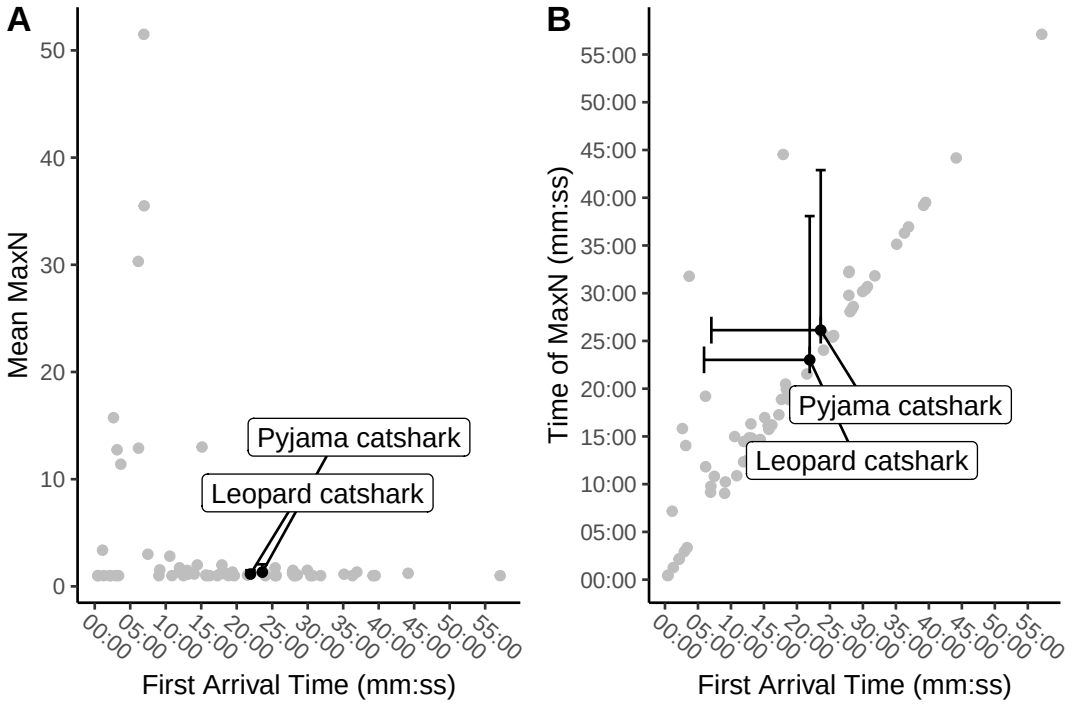


Figure 3.7: Mean Time of First Arrival time compared to (A) mean MaxN and (B) mean time of MaxN, with a focus on the study species *Poroderma* spp.

between yearly quarters were not significant (ANOVA: F = 1.654, p = 0.262).

The quarterly RA of *P. pantherinum* were lower than *P. africanum*, but remained relatively stable throughout the study period, and showed no significant differences amongst yearly quarters (ANOVA: F = 3.561, p = 0.075).

3.3.6 Effect of Environmental Variables

Binomial generalized linear models best-fitting the data indicated that the presence of *P. africanum* was influenced by SST, lunar phase and tide height (Figure 3.9, AIC = 233.1). The resulting graph determined that the presence of *P. africanum* had a significant negative correlation with SST (z = -3.363, p < 0.001), having a higher probability of occurring at lower temperatures (14 - 16 °C) rather than higher temperature (20 - 22 °C); a non-significant correlation with lunar phase (z = 1.55, p = 0.121); and a positive correlation with tide (z = 2.676, p < 0.01), with a higher probability of sightings at high tides.

Table 3.3: Summary of the Relative Abundance of the two *Poroderma* spp. in Mossel Bay, South Africa, between 2015 and 2018: Overall, seasonal, and quarterly.

Season	Quarter	*P. africanum*	*P. pantherinum*
Total		0.52	0.20
Summer		0.37	0.14
	1	0.40	0.13
	2	0.67	0.22
Winter		0.66	0.25
	3	0.88	0.31
	4	0.38	0.13

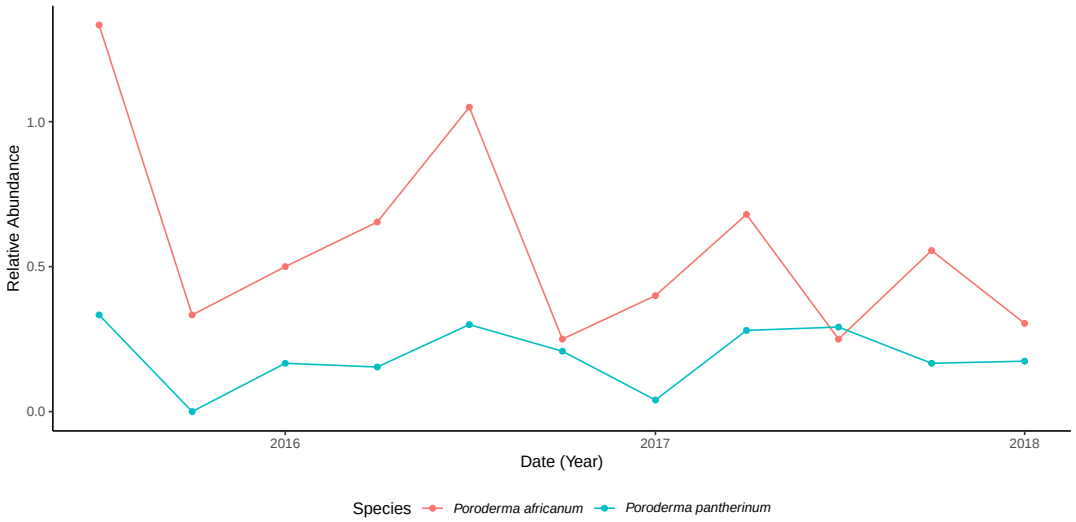
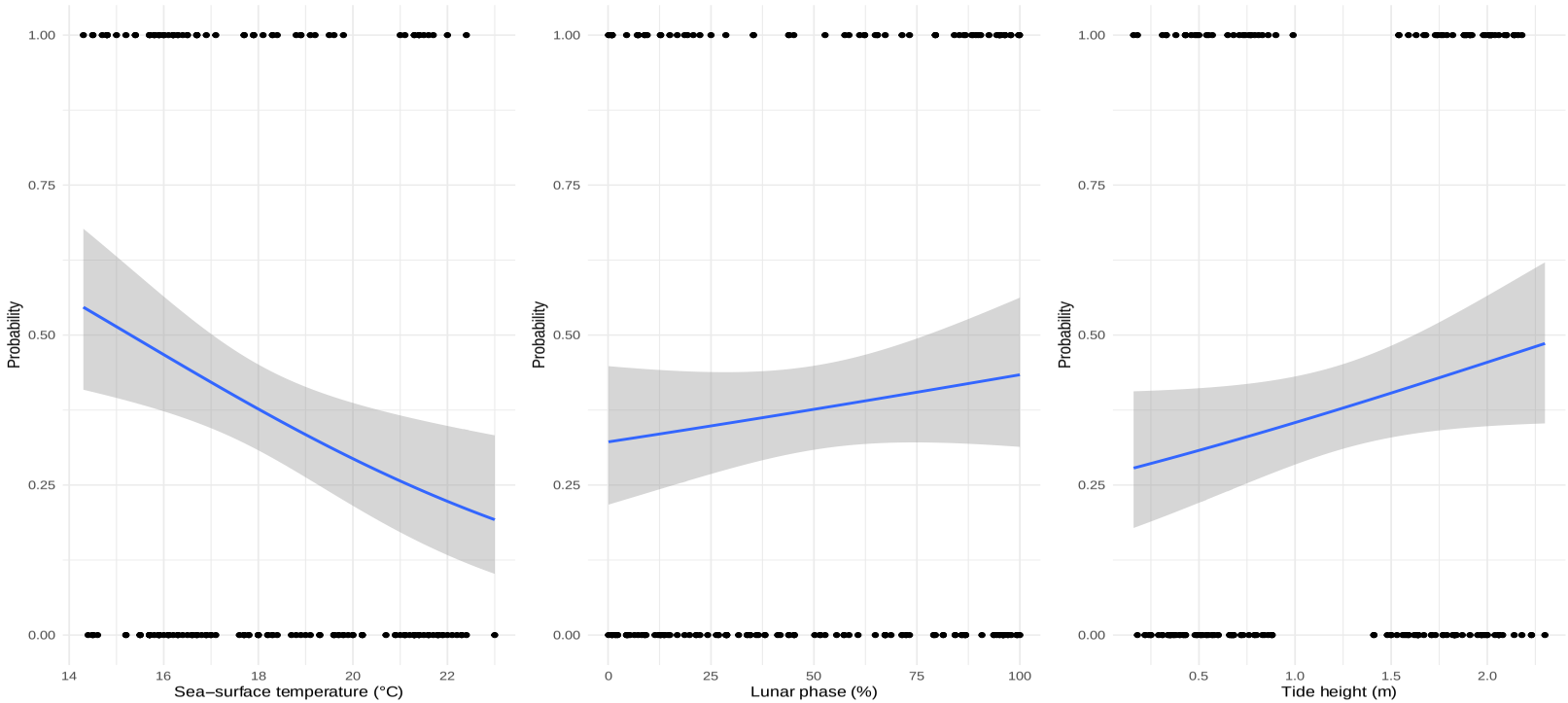


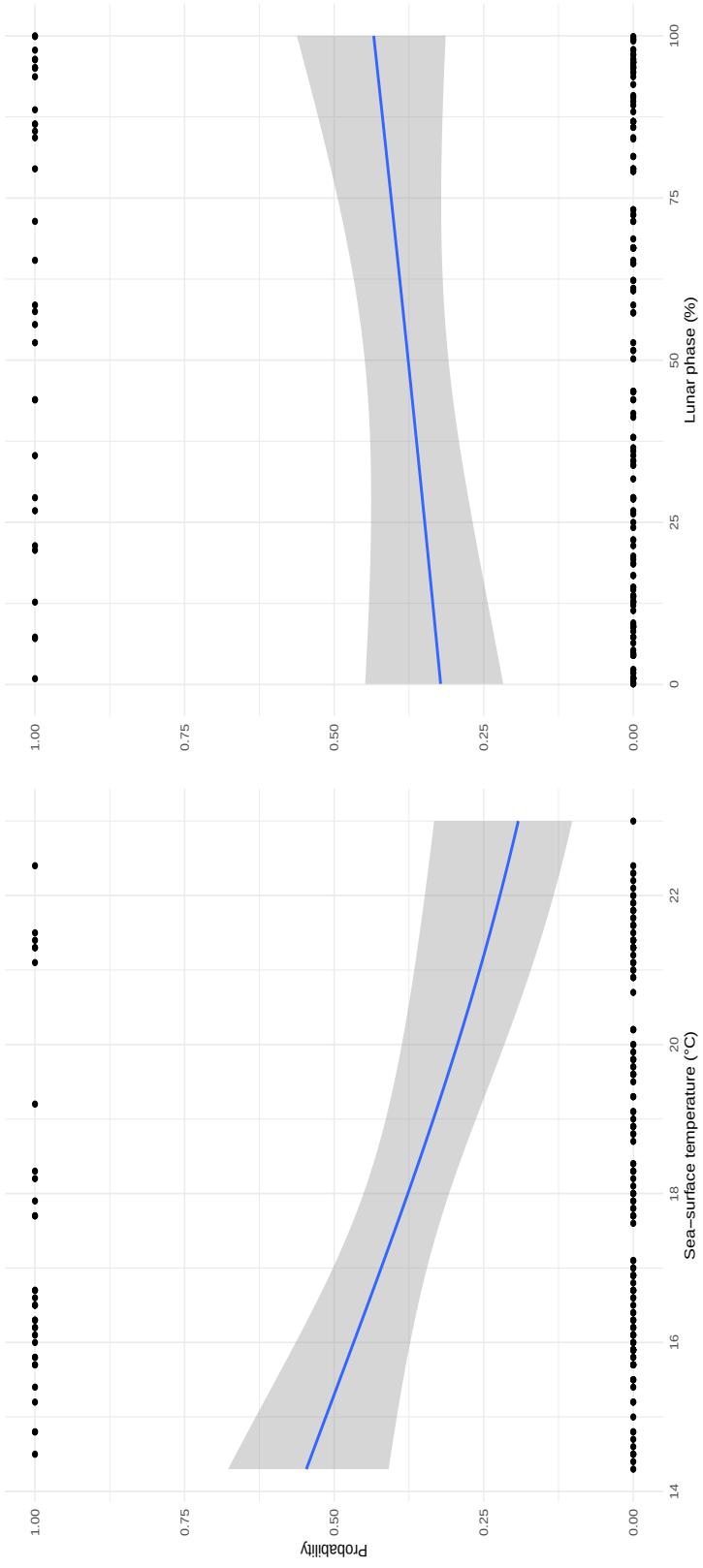
Figure 3.8: Quartely Relative Abundance of the two *Poroderma* spp. in Mossel Bay, South Africa, between 2015 and 2018.

The binomial generalized linear models determined that *P. pantherinum* was influenced by a combination of the SST (z = -2.088, $p < 0.05$) and lunar phase (z = 2.287, $p < 0.05$; Figure 3.10, AIC = 166.1). Similar to *P. africanum*, *P. pantherinum* had a higher probability of occurring at lower SST (14 - 16 °C). The probability of *P. pantherinum* presence was also significantly influenced by the phase of the moon, with the species having a higher probability of occurring at a fuller moon (lunar phase >80%).



	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.678	1.237	2.164	0.03
SST	–0.242	0.072	–3.363	0.001
Lunar (%)	0.007	0.005	1.55	0.121
Tide	0.658	0.246	2.676	0.007

Figure 3.9: Binomial probability plots of *P. africanum* in relation to SST (°C), lunar phase (%) and tide height (m).



	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.995	1.571	0.633	0.527
SST	−0.185	0.089	−2.088	0.037
Lunar (%)	0.014	0.006	2.287	0.022

Figure 3.10: Binomial probability plots of *P. pantherinum* in relation to SST (°C) and lunar phase (%).

3.3.7 Co-occurrence Analysis

Examination of co-occurrence between the 65 species identified, resulted in 2080 pair combinations. Of these, 1419 pairs (68.2%) were discarded because the expected co-occurrence was less than 1 (Veech, 2013). As a result, 661 pairs were analyzed (Figure 3.11). Of these, 116 pairs were non-random associated. Twenty-two pairs occurred together less often than would be expected if they were occurring randomly relative to one another (negatively associated), while 94 pairs occurred more often than randomly (positively associated).

The co-occurrence analysis included six out of the 12 chondrichthyan species seen on the BRUV deployments: *Aetomylaeus bovinus* (duckbill ray), *Bathytoshia brevicaudata* (short-tailed stingray), *Mustelus mustelus* (smoothhound), *H. edwardsii*, and both *Poroderma* species. *Bathytoshia brevicaudata* was only positively associated with *P. africanum*. The three Scyliorhinidae species occurred together more often than if they were distributed randomly relative to one another.

Poroderma africanum was detected in 77 deployments and had non-random associations with 6 other species. The species was positively associated with *P. pantherinum* (21 observed co-occurrences against 13.3 expected co-occurrences, $p < 0.01$), *H. edwardsii* (49 observed against 42.6 expected, $p < 0.05$) and *B. brevicaudata* (9 observed against 5.5 expected, $p < 0.05$), while *P. africanum* showed negative associations with *Chirodactylus brachydactylus* (twotone fingerfin; 27 observed against 34 expected, $p < 0.05$), *S. salpa* (56 observed against 62.1 expected, $p < 0.05$) and *A. pusillus pusillus* (2 observed against 5.9 expected, $p < 0.05$).

Poroderma pantherinum was detected in 34 deployments and had non-random associations with 4 other species. Apart from the positive association with *P. africanum*, *P. pantherinum* was positively associated with *H. edwardsii* (26 observed co-occurrences against 18.8 expected, $p < 0.01$). *Poroderma*

pantherinum was negatively associated with *Cheimerius nufar* (santer; 7 against 14.3, $p < 0.01$) and *Chaetodon marleyi* (doublesash butterflyfish; 3 against 6.9, $p < 0.05$).

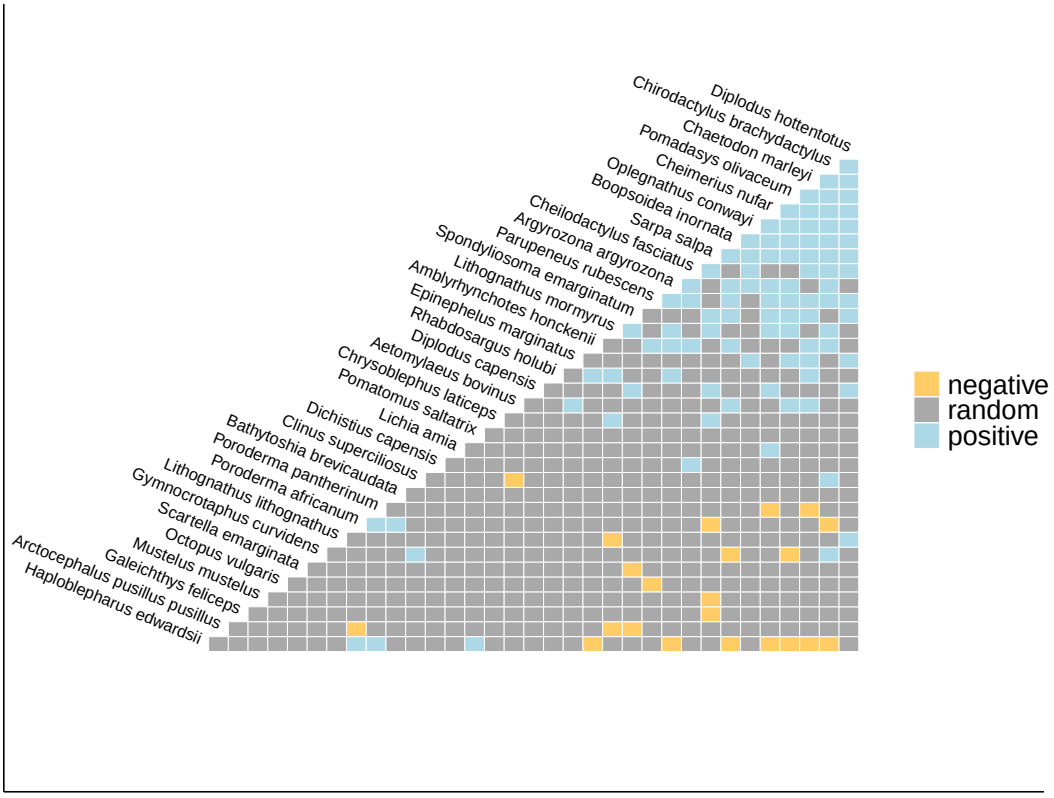


Figure 3.11: The species co-occurrence matrix showing the positive, negative and random species associations for Mossel Bay ichthyofauna. Scientific names are positioned to indicate the columns and rows that represent their pairwise relationships with other species.

The two *Poroderma* spp. co-occurred together 21 times, more often than would be normally expected (expected co-occurrence of 13.3 against 21 observed). There was a probability of 0.067 of both species being detected in the same camera deployment. This probability was 180^{th} out of the 661 co-occurrences examined (27.23%), 47^{th} of co-occurrences involving chondrichthyans (n = 210, 22.38%), and third of co-occurrences between chondrichthyans only (n = 18, 16.67%).

The co-occurrence network generated a network of 34 species (visualized as

vertices, Figure 3.12) with an Edge Density (ED) of 0.1. The MDS strain-model layout generated a network with higher trophic level animals (*P. africanum*, *P. pantherinum*, *B. brevicaudata*) towards the top of the network, while similar lower trophic level animals clustered towards the centre.

Positively- and negatively-associated species pairs were isolated and the Eigenvector Centrality (EC) scores were used to determine the gregariousness of these species. This identified the *C. marleyi* and *C. brachydactylus* as the most social species (EC = 1 and EC = 1, respectively). These two species were followed by *P. olivaceum* (EC = 0.99), *C. nufar* (EC = 0.96) and *B. inornata* (EC = 0.95). The study species *P. africanum* and *P. pantherinum* showed EC scores far lower, with values of 0.141 and 0.14, respectively. Other chondrichthyan species were more gregarious than the study species (*H. edwardsii*: EC = 0.33; *A. bovinus*: EC = 0.33), while other chondrichthyan species had lower gregariousness, such as *M. mustelus* (EC = 0.04) and *B. brevicaudata* (EC = 0.01).

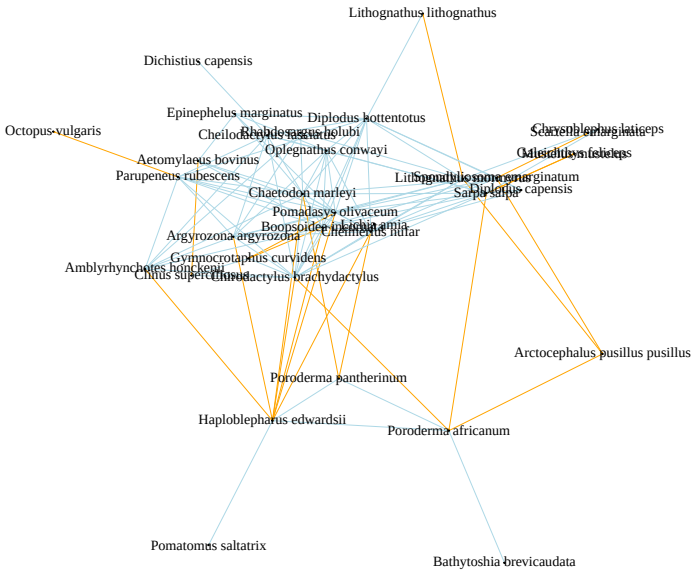


Figure 3.12: Co-occurrence network of non-random associated species in Mossel Bay. The network was displayed using an MDS strain-model layout algorithm. Positive co-occurrences = lightblue, negative co-occurrences = orange.

3.4 Discussion

Poroderma africanum and *P. pantherinum* were the second and third most abundant chondrichthyan species at the study site, while *H. edwardsii* was the most abundant. While *P. africanum* was more abundant across the three target reefs than *P. pantherinum*, there was no significant variation within the two species across the reefs. Several studies were performed over multiple years, but this is the first study to track the relative abundance of both *Poroderma* spp. over subsequent years using BRUVs. The RA of *P. pantherinum* remained relatively stable during this study with an RA = 0.19. However, the results did show a seasonal variation in RA of *P. africanum*. This was similar to a study in False Bay, where *P. africanum* also showed seasonal variation in abundance (de Vos *et al.*,

2015). The austral summer abundances (October-March) were similar for *P. africanum* across years, suggesting a low, but not a complete absence in the area. Results showed winter abundances decline consistently throughout the study, from RA = 1.33 to RA = 0.25. Declining *P. africanum* numbers corroborate a similar pattern to the results found in Grusd *et al.* (2019), which through mark-recapture noted declining abundance of *P. africanum* between 2013 and 2016 in Mossel Bay. While examined across two methods, the continuous decline of *P. africanum* in Mossel Bay between 2013 and 2018 warrants further examination.

Examination of the co-occurrence data indicated that the two *Poroderma* spp. were positively associated with one another, ranking third of co-occurrences between chondrichthyans. They co-occurred more often than if their distribution/presence overlapped randomly. An antagonistic relationship between the two species will likely result in a negative co-occurrence between the species, as they will be more likely to show small-scale spatial avoidance to avoid competition (REF), this suggests a potential non-aggressive co-occurrence between the two species. The positive association between *P. africanum* and *P. pantherinum* can be explained by the similar habitat and environmental requirements of these two species. Despite cephalopods making up a large part of *P. pantherinum*'s diet (Chapter 4), no aggressive encounters were documented between *O. vulgaris* and *P. pantherinum*. While *Poroderma* spp. are found in the presence of other conspecifics, the species are relatively solitary and their co-occurrence with other fish species is likely as a result of their attraction to the bait.

Various BRUV studies have been performed within the distributional range of the *Poroderma* spp. The RA values of *P. africanum* and *P. pantherinum* in this study were similar to the results from other studies (de Vos *et al.*, 2015; Table 3.5), with the former being at least twice as abundant during winter months compared with the latter, while being relatively equal in abundance during summer months.

Table 3.5: Sightings of *Poroderma* spp. in other BRUV studies around South Africa.

Source	**Site**	**Season**	**Variable**	***P. africanum***	***P. pantherinum***
Bernard and Götz (2012)	Tsitsikamma NP MPA	Yearly	Frequency	15/28	
de Vos *et al.* (2014)	Stilbaai MPA	Summer	RA	0.59	0.72
de Vos *et al.* (2015)	False Bay	Summer	RA	0.40	0.22
		Winter	RA	0.89	0.18
Roberson *et al.* (2015)	Betty's Bay MPA	Summer	RA	1.91	0.91
Parker (2015)	Tsitsikamma NP MPA	Yearly	Frequency	38/48	3/48
Juby (2016)	Algoa Bay (Shallow)	NA	MaxN	Day: 3 ± 1.3	Day: 1.5 ± 0.7
				Night: 2.4 ± 0.9	Night: 1.8 ± 0.8
	Algoa Bay (Deep)	NA	MaxN	Day: 1.7 ± 0.7	Day: 1.2 ± 0.4
				Night: 1.8 ± 0.8	Night: 1.1 ± 0.3
Schmidt (2018)	Tsitsikamma NP MPA	Summer	%O	Shallow Reef: 27.03 %	Shallow Reef: 33.33 %
				Deep Reef: 64.86 %	Deep Reef: 66.67 %
Osgood *et al.* (2019)	Walker Bay	Yearly	MaxN	1.90	1.30
Dando (2020)	Goukamma MPA	2013–2017	RA	1.96	0.47
Cortelezzi *et al.* (2022)	Robberg MPA	Summer	Frequency	MPA: 0.026	
				Exploited: 0.075	
This study	Mossel Bay	Yearly	RA	0.52	0.20
		Summer	RA	0.37	0.14
		Winter	RA	0.66	0.25

Due to sampling saturation, MaxN could be an inappropriate metric to document changes in abundances (Stobart *et al.*, 2015), and this is a concern with large schooling elasmobranch species (Kilfoil *et al.*, 2017). While oversaturation of certain abundant bream species might have influenced the detection and identification of new species, possibly underestimating the diversity along these reefs, undercounting the two *Poroderma* species was unlikely due to their behavioural response to either directly interact with, or approach close to the bait canister. The study species often came close to the BRUV rig to examine the bait canister and were undeterred by other species present. Due to this behaviour, their non-schooling behaviour, and relatively low abundance (max MaxN of 5 for *P. africanum*), *P. africanum* and *P. pantherinum* were not subject to sampling saturation, and as a result RA could be considered an appropriate metric to document increases or decreases in abundance of these species over time.

While changes in abundances should be corroborated through multiple methods (Schramm *et al.*, 2020), the decline of *P. africanum* in both this study and Grusd *et al.* (2019) is of concern for this local population. Further exploration on this species in Mossel Bay is needed, both to determine whether this trend is consistent in methods other than BRUVs or mark-recapture, and whether this decline is as a result of the removal of individuals (exploitation) out of the ecosystem or as a result of a shift in distribution.

The declining abundance of *P. africanum* and the low abundance of larger sharks within the fish assemblage of Mossel Bay is of concern for the ecological health of the ecosystem. While the conservation framework for the protection of the *Poroderma* spp., and by extension scyliorhinidae, is still up for debate (Osgood *et al.*, 2020; Chapter 6), the use of long-term BRUV surveys for abundance and biodiversity trends has been suggested to benefit future research of elasmobranchs (Murray *et al.*, 2019). Long-term abundance data, in combination with movement behaviour data (Chapter 5), would provide vital information to guide strategic

policy recommendations for elasmobranch conservation throughout South Africa.

In general the BRUV deployments provided insight into the ichthyofaunal assemblage at three shallow reefs in Mossel Bay, and the representation of the *Poroderma* spp. within the assemblage. Similar to other BRUV studies performed around South Africa, sparids were the most abundant fish family present (Bernard and Götz, 2012; de Vos *et al.*, 2014; Parker *et al.*, 2016; Dando, 2020). While the fish community structure showed a small significant difference between the different reef sites, the same species (*S. salpa*, *B. inornata*, *Spondyliosoma emarginatum* (Steentjie) and *P. olivaceum*) contributed the most to the differences between the three sites. This suggests that variation in abundance of the most dominant fish species was most likely the driver of the differences between the three reefs. There was a strong annual variation in fish species composition. However, as the top five species contributing to the differences in species composition between the years were present in all years, this suggests that this was driven by changes in abundance of these species, rather than a difference in species diversity.

The differences between Mitch and Roman's Reef compared to Darwin Reef were strongly correlated to SST and barometric pressure. The geographical location of Darwin Reef at the edge of the Cape St. Blaize peninsula near the open sea may explain the dissimilarity compared with Mitch and Roman's Reef. The influence of SST on the species composition within locations can be explained by seasonal changes, with species being sighted more frequently during certain times of the year (as seen with *P. africanum*). Several environmental factors such as current and wave-action have been shown to influence have been shown to influence nearshore fish assemblage (Shah Esmaeili *et al.*, 2022). It is feasible that the varying species diversity of the deployments could be explained by factors not considered during this study.

The average Shannon-Wiener diversity index of the fish assemblage in this study

(H' = 1.53) were similar to another BRUV study in the same bioregion, False Bay, which has the same reef geology and also a long history of fishing (H' = 1.4, Carr, 2014; Pfaff *et al.*, 2019). These indices were lower compared with those of other BRUV studies performed around South Africa (e.g., Tsitsikamma National Park: H' = 1.69, Parker *et al.*, 2016; Stilbaai MPA: H' = 1.9, de Vos *et al.*, 2014). This can be explained as these latter studies were performed in MPAs. While diversity indices are not an appropriate proxy to determine the state of a marine ecosystem in comparison to MPAs, this does suggests that protection of marine habitats can positively influence biodiversity indices. However, control sites would need to be included in the analysis within each study in order to confirm this relationship to rule out any other potential factors that may be contributing to the observed differences in diversity. Nevertheless, marine biodiversity seems to benefit more from fully enforced protection (Claudet *et al.*, 2020), rather than a complex of different protection classifications as seen around South Africa (i.e., no-take, controlled fishing permitted, or benthic protection; Kirkman *et al.*, 2021).

There was a significant difference in the fish biodiversity between quarters and seasons, with the diversity in the warmer summer months (January to March) being higher, which correlates with an increase of SST during this time of the year. Temperature and migration have both been shown to have influences on fish diversity (Fisher *et al.*, 2008; Tittensor *et al.*, 2010; Liang *et al.*, 2020), with intra-annual changes in water temperature serving as a possible cue for spawning (Rooker *et al.*, 1997).

The number of sightings of larger sharks was lower compared with similar BRUV surveys performed in the Stilbaai MPA (de Vos *et al.*, 2014) and Tsistikamma MPA (Bernard and Götz, 2012). However, the low number of sightings in this study concurs with BRUV studies done elsewhere around the coast in non-protected areas (de Vos *et al.*, 2015; Osgood *et al.*, 2019). While these are suggestive of the impact of shark fisheries around the coast (da Silva *et al.*,

2015), studies have highlighted the ineffectiveness of BRUVs in monitoring large shark species (Brooks *et al.*, 2011; Santana-Garcon *et al.*, 2014). To further examine the abundance of larger sharks in the area, additional research, including fisheries catch data, would need to be performed.

While SST and barometric pressure had strong influences on the biodiversity of the three reefs, the main environmental factors that influenced the presence of *P. africanum* were SST, lunar phase and tide height. This species had higher RA values at lower temperatures (14 - 16 °C), higher tides, and a greater (but non-significant) lunar phase. Similarly, the presence and absence of *P. pantherinum* were influenced by a combination of SST and lunar phase. *Poroderma pantherinum* was less likely to be present at higher water temperatures (20 - 22 °C) and was more likely to be sighted during greater lunar phase.

Thermal limits to distribution exists in many marine species across taxonomic classes (Stuart-Smith *et al.*, 2017). One of the main hypotheses of the limited geographic distribution of *Poroderma* spp. is the extreme temperatures on either side of southern Africa, with temperatures dropping below 13 °C along the west coast, and over 27 °C further along the east coast (Carr *et al.*, 2021). During the study period, the satellite-derived SST in Mossel Bay ranged from 13.9 °C to 24.5 °C. Temperatures outside this thermal range, as seen on either side of southern Africa, were not detected in Mossel Bay. It remains uncertain how temperatures outside the 13.9 °C and 24.5 °C range influence the movement behaviour of Poroderma spp. The results from this study, and in False Bay, indicated that both species preferred the lower ranges of the temperatures experienced (False Bay: 14 °C to 22.5 °C, Dufois and Rouault, 2012).

The phase of the moon has been shown to influence the behaviour of multiple marine species, such as *Epinephelus morio* (Red grouper) being more likely caught during the new moon (Pulver, 2017), large aggregations of *Caranx ignobilis* (giant trevally) arriving at Ponta do Ouro Partial Marine Reserve in southern

Mozambique around the full moon (Daly *et al.*, 2018), or *C. carcharadon* sightings increased at new moon and were typically lowest at full moon around two beaches in False Bay, South Africa (Weltz *et al.*, 2013). The presence of both *Poroderma* spp. were similarly influenced by lunar phase, and were more likely sighted during full moon. This could be potentially the result of more favorable conditions during nocturnal hunting excursions (see Chapter 5). Additionally, *P. africanum* was influenced by tide height as well, which is correlated to the lunar phase. This is seen in other species as well, such as the *Pomadasys commersonnii* (spotted grunter), whose estuarine presence were strongly correlated with tidal phases (Childs *et al.*, 2008). *Poroderma africanum*'s low presence during low tide can also be correlated to increased wave actions on shallow reefs.

While both *Poroderma* spp. are thought to be nocturnal (Mann, 2013), and fish community structures are known to differ between day and night (Harvey *et al.*, 2012), this was not explored during this study, due to the potentially hazardous conditions while operating a boat at night over shallow reef habit. Nocturnal surveys would additionally require specialized lighting equipment due to low-light surroundings underwater. An acoustic telemetry study did confirm the *Poroderma*'s nocturnal habits, which is further discussed in Chapters 5 and 6. The increased probability of *P. pantherinum* sightings during a higher lunar phase may be associated with improved foraging opportunities, providing brighter hunting opportunities for their preferred prey (i.e., cephalopods; Chapter 4). This could be further explored through the inclusion of nocturnal deployments. Diel variation in abundance was examined in Algoa Bay (Juby, 2016), and indicated that *P. pantherinum* was indeed nocturnal. This could suggest that the RA values of *P. pantherinum* in Mossel Bay could be higher than recorded in this study. However, *P. africanum* showed no significant variation in abundance between day and night (Juby, 2016). As the abundance of both species seems to vary between various

locations, more nocturnal studies are required to determine whether the disparity between diurnal and nocturnal periods is the same across their distribution ranges.

The results of this study indicated that both *P. africanum* and *P. pantherinum* co-occurred in the Mossel Bay area throughout the 2.5 year study period. *Poroderma pantherinum* showed a stable, but relatively lower, seasonal abundance across the years, while *P. africanum* showed a higher abundance during the winter months. Both SST and lunar phase were shown to have an influence on the presence of both species, while the presence of *P. africanum* was additionally influenced by tidal height. This indicates that while both species were influenced by similar environmental variables, there was a temporal variance in abundances between the two species. Depending on other factors, such as trophic niche separation, the varying abundances between seasons could alleviate potential conflict between the two *Poroderma* species, by lessening competition for similar prey during certain periods of the year.

Chapter 4

Trophic Ecology, with a Focus on Dietary Spatial Variation, of *Poroderma* spp.

4.1 Introduction

To explore the trophic interactions between predators and prey within a community, it is not only necessary to quantify the vertical energy transfer through the trophic web, but also the degree of resource partitioning and competition between sympatric species. While few studies have assessed the variety of factors involved, resource partitioning has been suggested as a possible mechanism for the coexistence of predators (Navia *et al.*, 2016). Sympatric elasmobranchs have a high degree of dietary overlap (Navia *et al.*, 2016). Intra-specific dietary preferences in elasmobranchs have found trophic resource partitioning between different size classes and ontogenetic stages (Richardson *et al.*, 2000; van der Heever *et al.*, 2020). Species can occupy different trophic roles throughout ontogeny, and occupy different trophic levels during different life stages (Navia *et al.*, 2016). Ontogenetic shifts in diet influence food-web dynamics and facilitate the coexistence of sympatric species through resource partitioning (Sánchez-Hernández *et al.*, 2019).

Factors like feeding time (Woodland *et al.*, 2011), depth (Valls *et al.*, 2011), spatiotemporal segregation (Churchill *et al.*, 2015) and prey size (Vögler *et al.*, 2009), may promote the coexistence of species in marine habitats (Navia *et al.*, 2016).

The introduction of anthropogenic food sources could impact the trophic position and predation pressure of predators upon the ecosystem. Depending on the food source introduced, it could in turn alter the effort-reward paradigm of predators, as seen between captive and wild coyotes (*Canis latrans*; Parsons *et al.*, 2022) or wolves (Ciucci *et al.*, 2020). Changes in resource availability could influence predator resource use and ecological interactions (Beckmann and Berger, 2003; Ciucci *et al.*, 2020; Gámez and Harris, 2021; Parsons *et al.*, 2022), which in turn could impact competition between sympatric predators (Drouilly *et al.*, 2018). While the impact of anthropogenically introduced food sources on the diet and behaviour of predators has been explored in terrestrial ecosystems (e.g. Ciucci *et al.*, 2020; Gámez and Harris, 2021; Parsons *et al.*, 2022), this is still under-explored in marine ecosystems (Gračan *et al.*, 2017). Furthermore, the effects of competition between sympatric elasmobranchs are still poorly understood and would require further exploration (Papastamatiou *et al.*, 2006).

Elasmobranchs are primarily the highest trophic predators in their ecological niches in most marine ecosystems where they occur (Compagno, 1990). They prey mainly on marine animals, from zooplankton to whales (Motta and Wilga, 2001), and are predominantly carnivorous (Compagno, 1990). Even though elasmobranchs are predators, exceptions do occur, such as *Sphyrna tiburo* (bonnethead shark) which is capable of eating and digesting seagrass (Leigh *et al.*, 2018), or *Rhinobatus typus* (giant shovelnose ray) which shows indication that the macroalgae *Sargassum* forms part of its diet (Meekan *et al.*, 2022). Information regarding trophic interactions and position within a food web is necessary to understand the

ecological role of sharks. Additionally, analysis of the diet composition is of importance in studies on predation, competition, trophodynamics, and food webs (Amundsen *et al.*, 1996). Trophic studies provide additional information towards ecosystem analyses, and by extension extrapolate biological processes and fisheries interactions (Lopez *et al.*, 2010). Subsequently this can be used to approximate biomass and food consumption, quantify predator-prey relationships, and explore energy flow between different elements of the ecosystem (Lopez *et al.*, 2012). This can be used to determine the impact of different resources upon the community structure. The determination of such impacts are then used for the intergrated management of marine ecosystens (Lopez *et al.*, 2012).

Mid-level predators, known as mesopredators, occupy an intermediate position in the trophic web, linking apex predators to lower levels in a food web (Crooks and Soulé, 1999; Ritchie and Johnson, 2009), and form a vital part of the ecosystem (Vaudo and Heithaus, 2011). Mesopredators provide a diffuse predation risk within the community, whereby a diversity of species all prey upon lower prey populations but with high redundancy. As top-order predators are removed, predation pressure on mid-level predators is relieved, which can potentially result in population expansion (Crooks and Soulé, 1999; Myers *et al.*, 2007). The increased abundance of mid-level predators in turn leads to increased predation pressure on lower trophic prey (Crooks and Soulé, 1999). Apart from competing for the same resources, sympatric mesopredators can share common predators as well, influencing their abundances (Ferretti *et al.*, 2013).

Scyliohinidae are quintessential mesopredators, with the whole family occupying a trophic level between higher level predators and herbivorous fish (Cortes, 1999). The family predates on a wide variety of species, including mollusc, crustaceans, and teleosts (e.g., Ebert *et al.*, 1996; Wetherbee *et al.*, 2004; Mnasri *et al.*, 2012; van der Heever *et al.*, 2020), and as mesopredators, provide a generalized predation risk upon the ecosystem (Heupel *et al.*, 2014).

The feeding habits of sharks in relation to size, sex, habitat and seasonal shifts have been explored using stomach content analyses (e.g., *Carcharhinus brachyurus*, (Lucifora *et al.*, 2009); *R. typus*; *Carcharhinus cautus*, nervous shark; *Rhizoprionodon acutus*, milk shark; and *Negaprion acutidens*, sicklefin lemon shark (White *et al.*, 2004)). Dietary studies on mesopredatory scyliorhinidae have been performed on *Scyliorhinus canicula* (small-spotted catshark) in the Irish Sea (Lyle, 1983) and in the Cantabrian Sea together with *Galeus melastomus* (black mouth catshark; Olaso *et al.*, 2005).

In South Africa, the diets of scyliorhinidae species that have been explored include *Apristurus microps* (smalleye catshark), *Apristurus saldanha* (Saldanha catshark), undescribed *Apristurus* spp., *Galeus polli* (African sawtail catshark), *Scyliorhinus capensis* (yellowspotted catshark) and *Holohalaelurus regani* (Izak catshark; Ebert *et al.*, 1996; Richardson *et al.*, 2000; van der Heever *et al.*, 2020). The diets of *A. saldanha*, the undescribed *Apristurus* spp., and *G. polli* were dominated by teleost, but each species focused on different teleost species. The diet of *A. microps* showed a mix of teleost, crustaceans, cephalopods (Ebert *et al.*, 1996). *Scyliorhinus capensis* showed contrasting diets between Ebert *et al.* (1996) (a mix of teleosts and crustaceans) and van der Heever *et al.* (2020) (majority crustaceans, followed by cephalopods), which the latter addressed as potentially caused by differences in storage, identification, or changes in teleost prey abundance possibly arising from fishing (van der Heever *et al.*, 2020). The diet of *H. regani* was examined in all three studies, with Ebert *et al.* (1996) and Richardson *et al.* (2000) identifying a dominance of teleost, followed by crustaceans and cephalopods, while van der Heever *et al.* (2020) identified a mix of crustaceans and cephalopods.

Poroderma africanum and *Poroderma pantherinum* are two sympatric and endemic Scyliorhinidae species of South Africa. Morphologically the two species

are very similar, with *P. africanum* being slightly larger (maximum ∼100 cm TL) compared to *P. pantherinum* (maximum 84 cm TL), and the two species displaying different colour patterns. Research into the trophic ecology of *Poroderma* spp. has been limited, with only a few localized descriptions of *P. africanum*'s diet (Lechanteur and Griffiths, 2003) and ambush hunting strategies on egg-laying squid (Smale *et al.*, 1995, 2001). The diet of the *Poroderma* spp. have further only been described in broad, descriptive terms (Branch *et al.*, 2017), suggesting that the two species share a large trophic niche. Both *Poroderma* spp. have cuspid-shaped teeth (tricuspid and one- or five-cusped teeth for *P. africanum* and *P. pantherinum*, respectively) designed for grasping prey (Bass *et al.*, 1975; Compagno *et al.*, 1989), and swallow their prey either whole or in chunks (Lechanteur and Griffiths, 2003). Both *Poroderma* spp. are considered benthic macro-predators feeding on large motile reef prey (Lechanteur and Griffiths, 2003).

This chapter aimed to examine the diet of *P. africanum* and *P. pantherinum* from stomach contents collected using gastric lavage. This allowed for the identification of important food groups and an evaluation of the ecological role of the two species within the foodweb. By exploring the diet of these species across multiple locations within their range, spatial variation in diet and the trophic position of the two study species across different locations were explored. The primary research questions of this chapter were as followed:

- Are there significant inter- and intra-specific variation in diet composition between two sympatric, reef-associated elasmobranchs?
- Do co-occurring, sympatric elasmobranchs show ontogenetic changes in diet?
- Was there spatial variation in the diet composition of two elasmobranchs with overlapping distributions?
- Were there differences in the trophic levels of two sympatric, reef-associated elasmobranchs?

4.2 Methods

4.2.1 Sample Collection

Stomach samples were collected across several sites in the Mossel Bay and Walker Bay areas (Section 2.1; Figure 4.1) according to the method as described in Section 2.3.1. Note was made on whether the bait used to capture the individual was removed to avoid influencing the results through the actions of collecting the animals. The sample locations were all located close to shore (<15 m depth) and over reef habitats for the presence of *Poroderma* spp. and for the ease of accessibility. The inclusion of Walker Bay into this study allowed for a greater sample size, and the addition of examining the influence of a different geographic location on the diet composition of the two species.

4.2.2 Data Analysis

4.2.2.1 Diet Composition

Prey items were identified to the lowest possible taxonomic level, counted, blotted dry, and weighed. An item was classified as Bait if there were clear signs of human influence (e.g., knife-cuts), or if the item/species was foreign to the Scyliorhinidae's ecosystem (e.g., *Scomber japonicus*, Pacific chub mackerel, and *Sardinops sagax*). It was assumed that these dietary items represented discarded bait by fishermen. The numerical abundance (N_i) informs about the feeding behaviour of the species, the weight (W_i) reflects dietary nutritional value (Macdonald and Green, 1983), and occurrence (frequency of occurrence; F_i) describes the population-wide eating habits (Cortés, 1997).

To determine whether an adequate number of samples were collected to correctly describe the prey diversity for each species, cumulative prey curves were generated using R's `vegan`-package (Oksanen *et al.*, 2013). The curve would

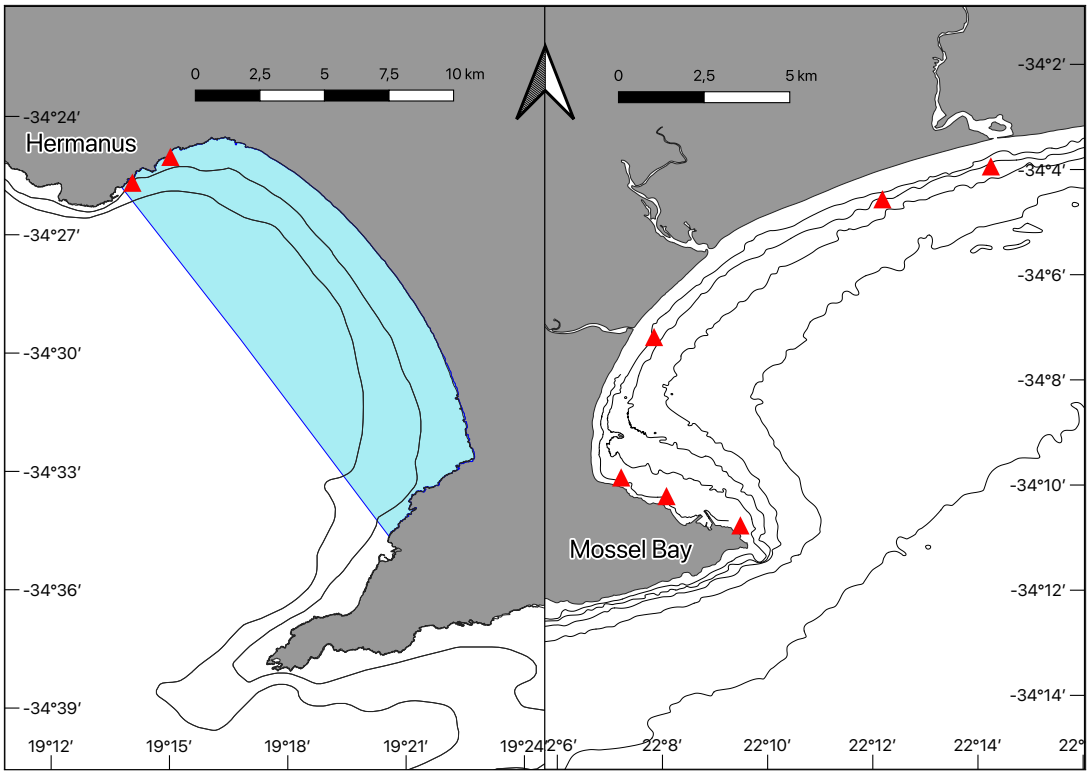


Figure 4.1: Map showing the locations of (A) Walker Bay and (B) Mossel Bay in the Western Cape Province, South Africa, with black triangles representing sampling locations of *Poroderma africanum* and *P. pantherinum* collected for gastric lavage. The light-blue region indicates the Walker Bay Whale Sanctuary. Created with qGIS v3.12.

indicate when a sufficient number of samples had been collected to accurately portray the species' diet, once the asymptote is reached (Ferry and Cailliet, 1996; Scenna *et al.*, 2006; Yick *et al.*, 2011). To exclude sampling order bias, the rarefaction analysis randomized the order in which the stomachs were analysed 100 times (Gotelli and Colwell, 2001). Linear regression was performed on the last four samples of the rarefaction curve, and the slope of the linear regression was statistically compared with a slope of 0 with a Student's t-test (see Equation 3.2.3). The test was performed on the last four values as this was indicative of a greater statistical power (Bizzarro *et al.*, 2007).

Each prey category was assessed according to abundance, weight in grams, and the number of stomachs that prey was found in. These variables were used to calculate the Index of Relative Importance (IRI; Equation 4.2.1, Pinkas *et al.*, 1971), and subsequently turned into the %IRI. %IRI values range from 0% to 100%, with lower values indicating low importance to the diet of the species, and higher values suggesting high importance to the diet.

$$IRI_i = (N_i + W_i) * F_i \qquad \text{(eq. 4.2.1)}$$

A feeding strategy plot was created to visualize the specialisation or generalisation of feeding strategies of the two *Poroderma* spp. To achieve this, weight as a percentage ($\%W_i$) of prey categories were plotted against Frequency of Occurrence ($\%F_i$) (Amundsen *et al.*, 1996). If a prey category falls in the upper left quadrant of the plot, it suggests specialization by few individuals in the population; while prey categories that fall in the upper right-side quadrant of the plot suggest specialisation by the population as a whole. Prey categories that fall on the lower half of the plot suggest generalization by the population, as they are eaten in low quantities (Amundsen *et al.*, 1996).

4.2.2.2 Inter- and intra-specific Differences in Trophic Niche

Pianka's niche overlap, $\hat{O}_{jk}$, (Equation 4.2.2, Winemiller and Pianka, 1990) and Schoener's overlap index, $\hat{P}_{jk}$, (Equation 4.2.3, Schoener, 1970) were calculated using the `spaa`-package in R (Zhang and Zhang, 2016), whereby p_{ij} indicated the proportion of resource i used by species j, p_{ik} indicated the proportion of resource i used by species k, and n is the total number of resource states. The resulting measures of overlap ranged from 0 with no resources used in common, to 1 with a complete overlap of resources.

$$\hat{O}_{jk} = \frac{\sum_{i}^{n} \hat{p}_{ij}\hat{p}_{ik}}{\sqrt{\sum_{i}^{n} \hat{p}_{ij}^2 \sum_{i}^{n} \hat{p}_{ik}^2}} \qquad \text{(eq. 4.2.2)}$$

$$\hat{P}_{jk} = [\sum_{i=1}^{n} (\text{minimum } \hat{p}_{ij}\hat{p}_{ik})] * 100 \qquad \text{(eq. 4.2.3)}$$

Levin's niche width ($\hat{B}$) was calculated for each species to quantify the trophic niche breadth (Krebs *et al.*, 1989, Equation 4.2.4) using the `spaa`-package (Zhang and Zhang, 2016). The niche width was subsequently standardized using Equation 4.2.5, where $\hat{B}_A$ is Levin's standardized niche breadth, and n is the number of possible resource states. Values ranged from 0 to 1, with low values indicating a specialist predator, while high values indicate a generalist diet (Krebs *et al.*, 1989).

$$\hat{B} = \frac{1}{\sum p_j^2} \qquad \text{(eq. 4.2.4)}$$

$$\hat{B}_A = \frac{\hat{B} - 1}{n - 1} \qquad \text{(eq. 4.2.5)}$$

Shannon-diversity indices (Equation 3.2.2) were used to explore the diversity of

stomach content across the different size classes, with the proportion of individual stomach items. Here the total number of items per size class was used with p_i as the proportion of individual stomach items found (n_i) divided by the total number of stomach items found (N), and s the total number of size classes (Ludwig and Reynolds, 1988).

A multi-variate PERMANOVA was used to determine whether the diet composition differed significantly between species (*P. africanum* vs *P. pantherinum*), sexes (male vs female), sites (Mossel Bay vs Walker Bay) and sizes. The PERMANOVA was performed using the `adonis2` function from the `vegan` package (Oksanen *et al.*, 2013).

To examine how the stomach content differed between the two study species and geographic locations, a Principal Component Analysis (PCA) was performed on the square root of the stomach content count. Stomach contents were grouped into classes (i.e., Bivalve, Cephalopod, Chondrichthyan, Crustacean, Gastropod, Plant, Polychaete, and Teleost) to identify the relative importance of each class.

4.2.2.3 Ontogenetic Shifts in Diet

To explore the ontogenetic changes in diet, Total Length (TL) of the two study species were divided into different size classes. These were based on the size range of captured individuals, length at 50% maturity (Sections 1.5.1 and 1.5.2), and the maximum length of the species. Both species were grouped into size classes representing Small, Medium, Large and Extra-Large. Each size-class covered a range of 15 cm for *P. africanum* and 10 cm for *P. pantherinum* (Table 4.1), to cover the size-range of both species into an equal number of categories.

4.2.2.4 Trophic Level

The trophic level (TL_k) of the species was calculated based on the proportion of prey categories (Ebert and Bizzarro, 2007), and the trophic levels of the prey categories.

Table 4.1: Size-classes of both *Poroderma* spp. used to infer ontogenetic changes in the diet.

Size-Class	***P. africanum***	***P. pantherinum***
Small	<55 cm	<45 cm
Medium	55 - 70 cm	45 - 55 cm
Large	70 - 85 cm	55 - 65 cm
Extra-Large	>85 cm	>65 cm

$$TL_k = 1 + (\sum_{j=1}^{n} P_{jk} * TL_j) \qquad \text{(eq. 4.2.6)}$$

whereby n is the number of prey categories, P_{jk} proportion of prey category j in the diet of species k, and TL_j Trophic Level of prey category (Table 4.2, derived from Cortes, 1999; Ebert and Bizzarro, 2007).

Table 4.2: Standardized trophic levels of shark prey, derived from Cortes (1999); Ebert and Bizzarro (2007).

Group	**Description**	**Trophic Level**
MAM	Marine mammals (cetaceans, pinnipeds, mustelids)	4.02
BIR	Seabirds	3.87
CHOND	Chondrichthyan fishes	3.65
FISH	Teleost and agnathan fishes	3.24
CEPH	Octopi, squids, cuttlefishes, and unidentified cephalopods	3.20
AMPH	Amphipods and isopods	3.18
POLY	Polychaetes and other marine worms	2.60
DECA	Decapod crustaceans	2.52
INVERT	Other invertebrates (all invertebrates except molluscs, crustaceans, and zooplankton)	2.50
OCRUST	Other crustaceans and unidentified crustaceans	2.40
REP	Marine reptiles (sea turtles and sea snakes)	2.40
EUPH	Euphausiids and mysids	2.25
ZOO	Zooplankton (mainly euphausids “krill”)	2.20
MOLL	Molluscs (excluding cephalopods) and unidentified mollusks	2.10
PL	Plants (marine plants and algae)	1.00

4.3 Results

4.3.1 Diet Composition

Between July 2015 and April 2018, 177 *P. africanum* and 40 *P. pantherinum* were sampled in Mossel Bay and Walker Bay. This resulted in 124 and 36 stomach samples, respectively. There were 56 and 68 stomach samples for male and female *P. africanum*, respectively, and 20 and 16 stomach samples for male and female *P. pantherinum*, respectively. A total of 80 *P. africanum* stomach samples were collected in Mossel Bay, and 44 stomach samples in Walker Bay. A total of 15 *P. pantherinum* stomach samples were collected in Mossel Bay, and 21 stomach samples in Walker Bay. Sizes for *P. africanum* ranged from 40 cm TL to 99 cm TL, while the sizes for *P. pantherinum* ranged from 38 cm TL to 73.5 cm TL (Figure 4.2).

A rarefaction curve of stomach items was generated for both species, with stomach items classified as Bait grouped together (Figure 4.3). The curve of *P. africanum* reached a slope of 0.12, while the curve of *P. pantherinum* reached a slope of 0.31. The significance of the curve was quantitatively explored, with the end slope of the rarefaction curve compared with a slope of 0 (Student's t-test), however, both curves were significantly different from the 0-slope (*P. africanum*: $t = 427.97$, $p < 0.001$; *P. pantherinum*: $t = 9060.67$, $p < 0.001$).

The natural diet of *P. africanum* at the two locations was made up out of 36 items and consisted primarily of Teleost (22.69 %IRI) and *Octopus vulgaris* (Common octopus; 11.48 %IRI). However, a large portion of the species diet consisted of items classified as Bait[1], and these items (grouped) made up the majority of the *P. africanum* diet (64.54 %IRI). Closer examination of the diet by location revealed spatial variation between the populations. Bait dominated the

[1]Excluding the bait used to catch the species.

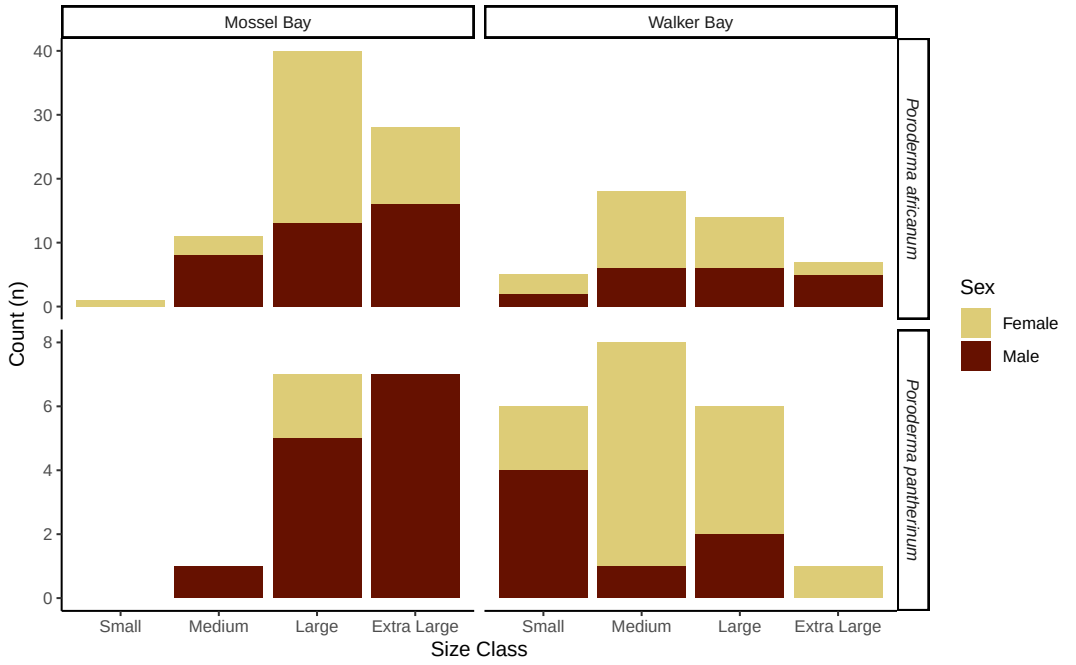


Figure 4.2: Distribution of the samples of sampled *P. africanum* and *P. pantherinum* across size classes split between sexes. The size classes for *P. africanum* are designated as: Small <55 cm TL, Medium 55-70 cm TL, Large 70-85 cm TL, Extra large >85 cm TL, while the size classes for *P. pantherinum* are designated as: Small <45 cm TL, Medium 45-55 cm TL, Large 55-65 cm TL, Extra large >65 cm TL.

diet of *P. africanum* only in Mossel Bay (73.19 %IRI, Table 4.3), while Teleost was the most abundant in the natural diet of *P. africanum* at both locations (Mossel Bay = 13.46 %IRI, Walker Bay = 77.96 %IRI, Table 4.4). The natural diet of *P. africanum* in Mossel Bay was followed by *O. vulgaris* (12.42 %IRI), compared to Walker Bay where the most dominant stomach content was followed by Crustacean (10.58 %IRI).

The results showed that a small number of individuals consumed a large amount of Bait, while the rest of the prey content was consumed in lower and more infrequent amounts (Figure 4.4). The occurrence of several indigestible items (e.g., stones, hard coral, fibres) suggest that they were ingested accidentally and were ignored during further analysis.

A total of 18 different items were found in the stomachs of *P. pantherinum*, and consisted predominantly of *O. vulgaris* (68.40 %IRI) and *Sepia* spp. (15.28 %IRI).

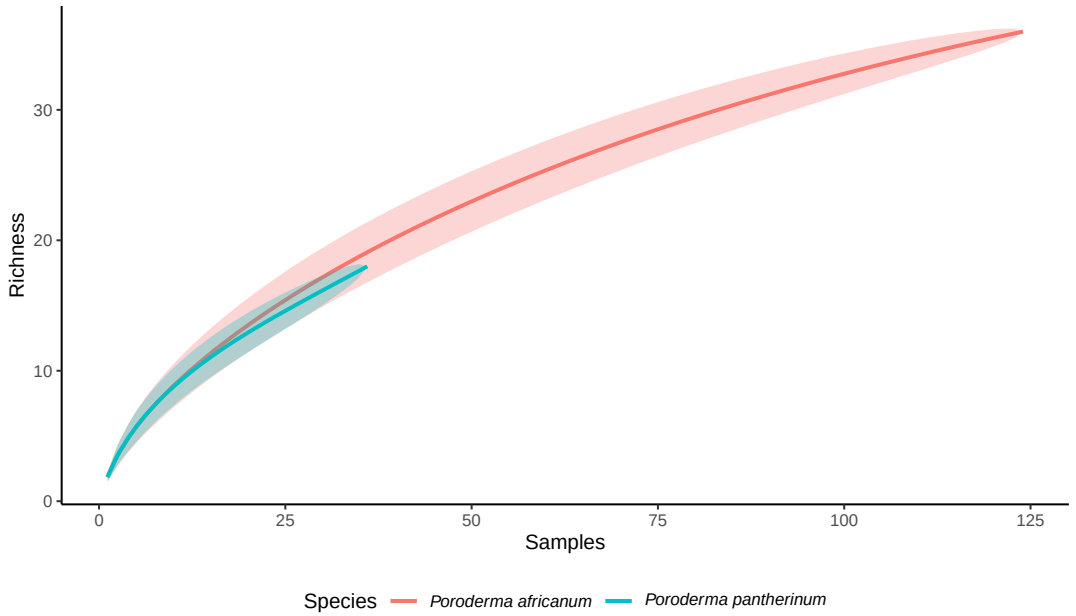


Figure 4.3: Rarefaction curve of richness in the diet of *Poroderma*. The shaded areas indicate the standard deviation around the mean number of cumulative prey categories for the number of stomach content samples analysed after 100 randomisations.

Stronger spatial variation was seen in the diet of *P. pantherinum*. The diet in Mossel Bay was dominated by *O. vulgaris* (68.13 %IRI, Table 4.5) and *Sepia* spp. (25.31 %IRI), while in Walker Bay stomach content consisted primarily of Teleost (39.9 %IRI) and *O. vulgaris* (27.3 %IRI), followed by Cephalopod (10.26 %IRI).

Results showed that approximately half of the sampled individuals had consumed Cephalopod, and which made up the highest amount of stomach content in weight (Figure 4.5). In contrast, food items classified as Bait comprised a small fraction (<10%) of the overall diet (1.31 %IRI) in *P. pantherinum*.

4.3.2 Inter- and intra-specific Differences in Trophic Niche

Pianka's niche-width overlap calculated from the %IRI determined that there was only a $\hat{O} = 0.3$ overlap between the diets of *P. africanum* and *P. pantherinum* (Table 4.7), indicating only a partial niche-overlap between the two species.

Table 4.3: Stomach items of *P. africanum* in Mossel Bay grouped by item, with bait grouped as a single item. Each item is described by number, weight, frequency of occurrence, Index of Relative Importance (IRI) and percentage Index of Relative Importance (%IRI).

Item	**Number**	**Weight**	**Frequency**	**IRI**	**% IRI**
Bait	38.00	1526.33	27	42236.91	73.19
Teleost	42.00	173.82	36	7769.70	13.46
Octopus vulgaris	19.00	379.25	18	7168.50	12.42
Sepia spp.	3.00	59.88	3	188.64	0.33
Crab	6.00	5.76	6	70.56	0.12
Callorhinchus capensis	1.00	51.00	1	52.00	0.09
Chirodactylus brachydactylus	1.00	49.20	1	50.20	0.09
Scartella emarginata	2.00	20.53	2	45.06	0.08
Acanthistius sebastoides	2.00	14.94	2	33.88	0.06
Chondrichthyan Egg	3.00	9.69	2	25.38	0.04
Cephalopod	2.00	9.10	2	22.20	0.04
Shell	5.00	0.07	2	10.13	0.02
Merluccius paradoxus	1.00	6.45	1	7.45	0.01
Hippocampus capensis	1.00	5.33	1	6.33	0.01
Diplodus capensis	1.00	5.15	1	6.15	0.01
Unknown	3.00	0.78	1	3.78	0.01
Galeichthys feliceps	1.00	2.68	1	3.68	0.01
Green algae	2.00	0.92	1	2.92	0.01
Plant	1.00	0.46	1	1.46	0.00
Tomicodon eos	1.00	0.46	1	1.46	0.00
Polychaete	1.00	0.16	1	1.16	0.00
Crustacean	1.00	0.04	1	1.04	0.00
Seaweed (Red)	1.00	0.01	1	1.01	0.00

Schoener's overlap index showed a similar overlap with $\hat{P}_{ij} = 0.25$. Levin's standardized niche width for both species was quite low, and suggested a more specialist behaviour ($B_A = 0.2$ and 0.03 for *P. africanum* and *P. pantherinum*, respectively).

The PERMANOVA indicated that species, size and location had significant influences on the differences in diet of the species ($F = 3.79$, $p < 0.01$; $F = 3.01$, $p < 0.01$; and $F = 3.16$, $p < 0.01$, respectively, Table 4.8).

The PCA on the stomach contents of both species grouped the stomach samples into several clusters along the top half of the PC2 axis, while the bottom

Table 4.4: Stomach items of *P. africanum* in Walker Bay grouped by item, with bait grouped as a single item. Each item is described by number, weight, frequency of occurrence, Index of Relative Importance (IRI) and percentage Index of Relative Importance (%IRI).

Item	**Number**	**Weight**	**Frequency**	**IRI**	**% IRI**
Teleost	26.00	52.18	23	1798.14	77.96
Crustacean	12.00	8.33	12	243.96	10.58
Bait	4.00	23.11	4	108.44	4.70
Octopus vulgaris	4.00	15.44	3	58.32	2.53
Cephalopod	3.00	4.57	3	22.71	0.98
Glycera spp.	3.00	4.96	2	15.92	0.69
Wonder worm	2.00	3.94	2	11.88	0.52
Seacatfish eggs	11.00	0.66	1	11.66	0.51
Jasus lalandii	2.00	1.56	2	7.12	0.31
Polychaeta	2.00	0.51	2	5.02	0.22
Algae	2.00	0.10	2	4.20	0.18
Loligo vulgaris reynaudii	2.00	2.02	1	4.02	0.17
Nereid	1.00	2.56	1	3.56	0.15
Nucella lapillus	1.00	1.46	1	2.46	0.11
Mazella	1.00	0.95	1	1.95	0.08
Crepidula fornicata	1.00	0.70	1	1.70	0.07
Green algae	1.00	0.35	1	1.35	0.06
Lice	1.00	0.13	1	1.13	0.05
Plant	1.00	0.06	1	1.06	0.05
Crab	1.00	0.01	1	1.01	0.04
Nematoda spp.	1.00	0.01	1	1.01	0.04

half of the PC2 axis showed less clustering of samples (Figure 4.6). The longest vectors (length >0.1 along either x- or y-axis) identified Teleost and Cephalopod as the main drivers for the clustered samples, while Crustacean was identified as the main driver for dispersed samples along the bottom half of the graph.

Table 4.5: Stomach items of *P. pantherinum* in Mossel Bay grouped by item, with bait grouped as a single item. Each item is described by number, weight, frequency of occurrence, Index of Relative Importance (IRI) and percentage Index of Relative Importance (%IRI).

Item	Number	Weight	Frequency	IRI	% IRI
Octopus vulgaris	13.00	85.23	10	982.30	68.13
Sepia spp.	4.00	87.24	4	364.96	25.31
Teleost	4.00	6.33	4	41.32	2.87
Bait	1.00	30.28	1	31.28	2.17
Crab	3.00	1.63	3	13.89	0.96
Clinus spp.	1.00	1.80	1	2.80	0.19
Oyster	1.00	0.64	1	1.64	0.11
Cephalopod	1.00	0.32	1	1.32	0.09
Whelk	1.00	0.30	1	1.30	0.09
Polychaete	1.00	0.00	1	1.00	0.07

Table 4.6: Stomach items of *P. pantherinum* in Walker Bay grouped by item, with bait grouped as a single item. Each item is described by number, weight, frequency of occurrence, Index of Relative Importance (IRI) and percentage Index of Relative Importance (%IRI).

Item	Number	Weight	Frequency	IRI	% IRI
Teleost	8.00	3.16	7	78.12	39.90
Octopus vulgaris	7.00	3.69	5	53.45	27.30
Cephalopod	4.00	1.02	4	20.08	10.26
Crustacean	4.00	0.20	4	16.80	8.58
Crab	2.00	3.43	2	10.86	5.55
Digested Content	3.00	0.21	3	9.63	4.92
Perna perna	1.00	0.56	1	1.56	0.80
Mollusc	1.00	0.20	1	1.20	0.61
Loligo vulgaris reynaudii	1.00	0.05	1	1.05	0.54
Nematoda spp.	1.00	0.01	1	1.01	0.52
Shell	1.00	0.01	1	1.01	0.52
Unknown	1.00	0.01	1	1.01	0.52

Table 4.7: Niche analysis, with light-grey coloured cells showing Levin's standardize niche breadth values (B_A), the lower-left cell Pianka's niche overlap ($\hat{O}$), and top-right Schoener overlap index ($\hat{P}_{ij}$).

	Poroderma africanum	***Poroderma pantherinum***
Poroderma africanum	$B_A = 0.2$	$\hat{P}_{ij} = 0.25$
Poroderma pantherinum	$\hat{O} = 0.3$	$B_A = 0.03$

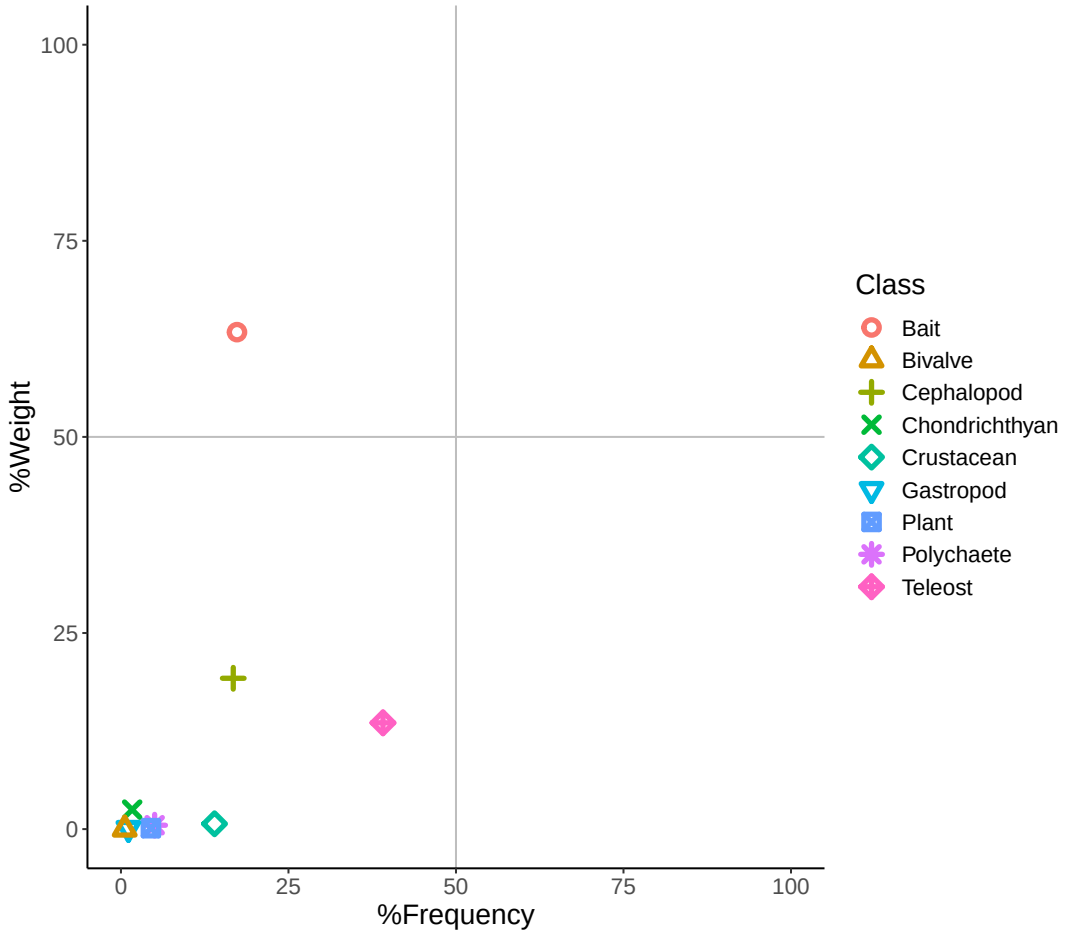


Figure 4.4: Feeding strategy plot of *P. africanum*. The x-axis represents the proportion of the population that eats the represented prey items, while the y-axis represents the proportion of prey items in weight. Upper quadrants represent prey items that are eaten in large quantities, while those in the lower quadrants are eaten in small amounts. The right quadrants represent prey items that are eaten by a large portion of the population, while those in the left are eaten by few individuals in the population.

Table 4.8: PERMANOVA results on stomach content collected from *P. africanum* and *P. pantherinum* between species, sex, site and size (TL). DF = degrees of freedom.

	Df	**SumsOfSqs**	**MeanSqs**	**F.Model**	**R2**	**Pr(>F)**
Species	1	1.48	1.48	3.79	0.02	0.0020
Site	1	1.23	1.23	3.16	0.02	0.0040
TL	1	1.17	1.17	3.01	0.02	0.0050
Sex	1	0.48	0.48	1.23	0.01	0.2660
Residuals	153	59.58	0.39		0.93	
Total	157	63.94			1.00	

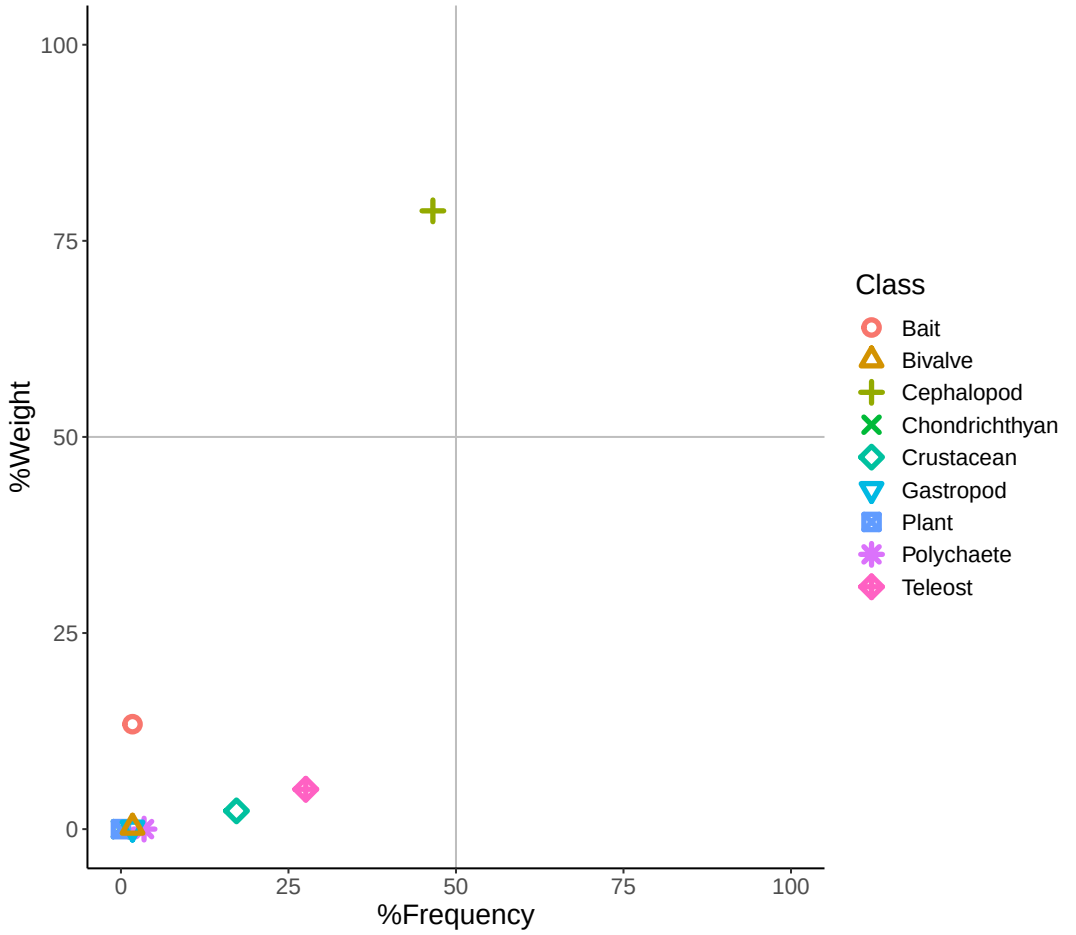


Figure 4.5: Feeding strategy plot of *P. pantherinum*. The x-axis represents the proportion of the population that eats the represented prey items, while the y-axis represents the proportion of prey items in weight. Upper quadrants represent prey items that are eaten in large quantities, while those in the lower quadrants are eaten in small amounts. The right quadrants represent prey items that are eaten by a large portion of the population, while those in the left are eaten by few individuals in the population.

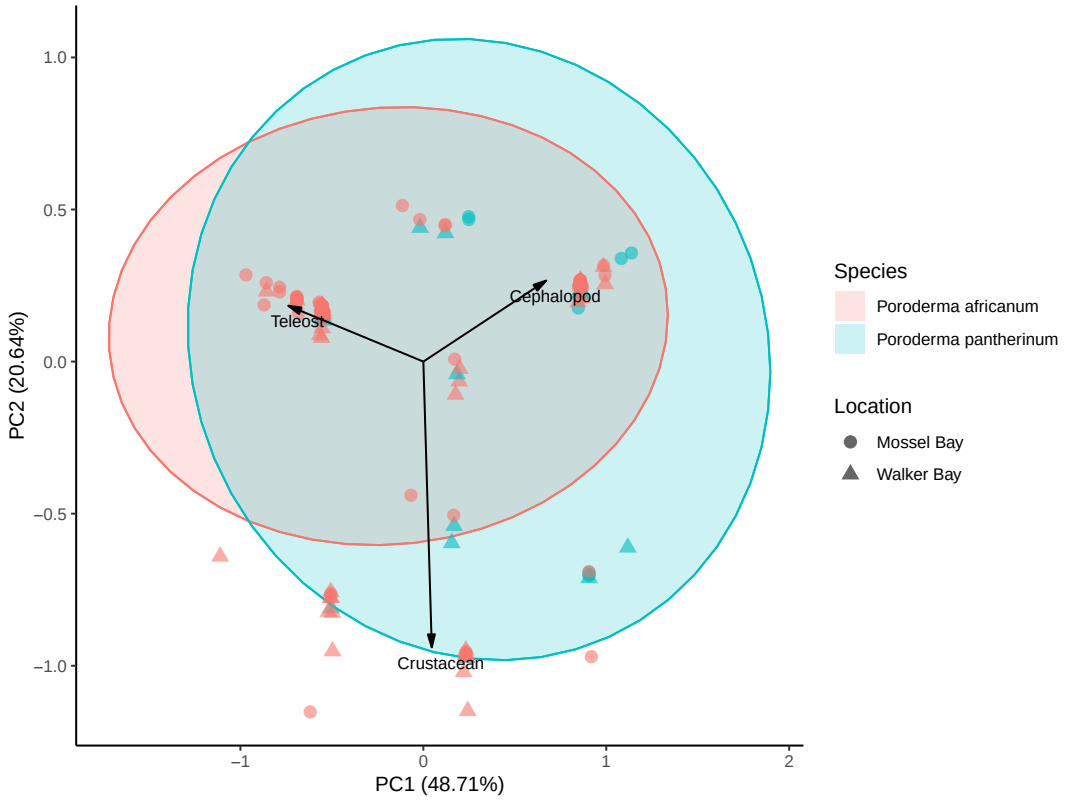


Figure 4.6: Principal Component Analysis plot of stomach content of *Poroderma* spp. from Walker Bay and Mossel Bay, with the vectors of the largest contributors to the stomach composition visualized (n=161).

4.3.3 Ontogenetic Shifts in Diet

Examination of the stomach content showed no Cephalopod in the diet of *P. africanum* in individuals smaller than 55 cm TL (Figure 4.7). Cephalopod made up only a small fraction of the diet in Medium and Large individuals (Medium: 6.32 %IRI, Large: 7.43 %IRI), and were the dominant component in the natural diet of Extra-Large individuals (36.51 %IRI). The proportion of Bait was consistent in all size classes (Small: 43.31 %IRI, Medium: 50.14 %IRI, Large: 45.23 %IRI Extra Large: 50.96 %IRI). The mean (± sd) across all size classes was 47.41 %IRI (± 3.72 %IRI). Crustacean made up a small fraction of the natural diet of Small to Medium individuals *P. africanum* (Small: 6.03 %IRI; Medium: 8.2 %IRI) and were practically absent from larger-sized individuals (Large: 0.91 %IRI, Extra Large: 0.11 %IRI). Examination of the diversity of items per size-class showed a peak of diversity in Medium individuals ($H' = 2.38$), with Small individuals showing the lowest diversity ($H' = 1.48$). The diversities of Large and Extra-Large individuals were $H' = 2.23$ and $H' = 2.13$, respectively.

Poroderma pantherinum showed an earlier ontogenetic shift in diet. The diet of Small individuals comprised of a mix of Cephalopod, Crustacean and Teleost (24.54 %IRI, 23.94 %IRI and 45.07 %IRI, respectively, Figure 4.8), while the diet of larger *P. pantherinum* (>55 cm TL) consisted predominantly of Cephalopod (Large: 95.77 %IRI, Extra Large: 89.44 %IRI). Large individuals showed the highest diversity of prey items ($H' = 1.52$), followed by Small individuals ($H' = 1.36$). Medium and Extra-Large individuals showed similar diversity indices ($H' = 1.96$ and $H' = 1.82$, respectively).

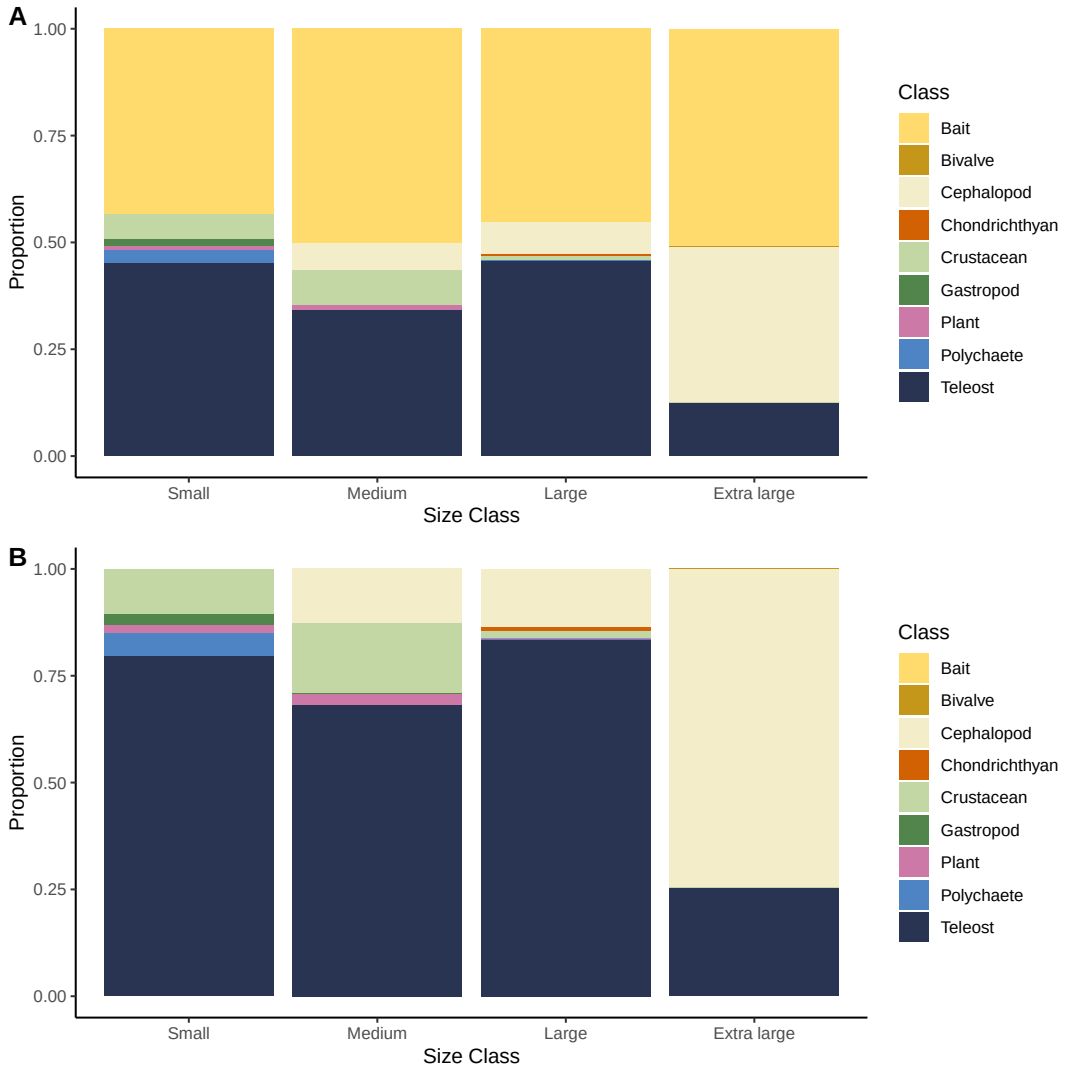


Figure 4.7: Proportion of stomach content of *P. africanum* (based on %IRI) across various size classes: Small <55 cm TL, Medium 55-70 cm TL, Large 70-85 cm TL, Extra large >85 cm TL. (A) Complete diet including bait, (B) natural diet.

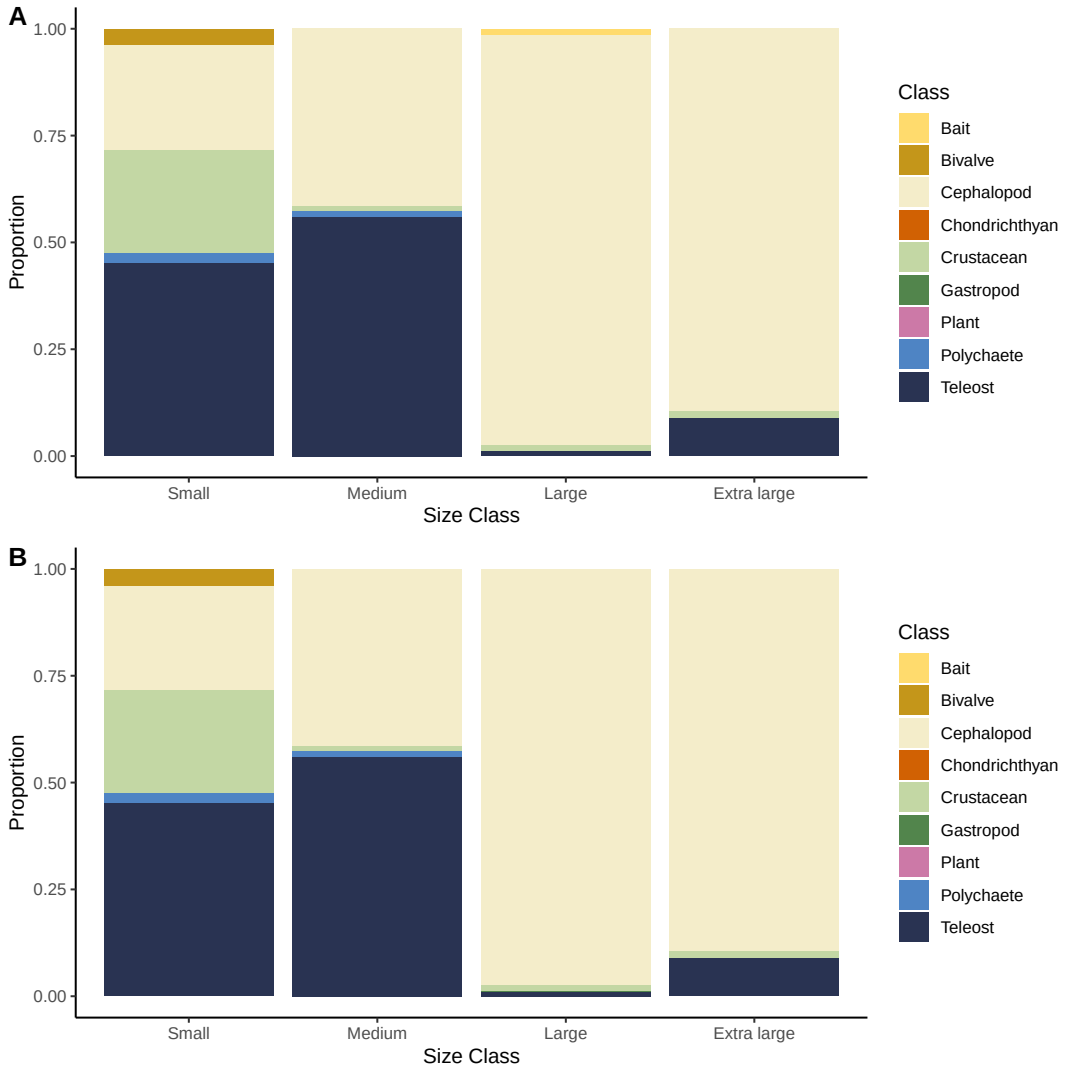


Figure 4.8: Proportion of stomach content of *P. pantherinum* (based on %IRI) across various size classes: Small <45 cm TL, Medium 45-55 cm TL, Large 55-65 cm TL, Extra large >65 cm TL. (A) Complete diet including bait, (B) natural diet.

4.3.4 Trophic Level

The trophic level of *P. africanum* and *P. pantherinum* were calculated based on 124 and 36 samples, respectively. P_j was based on the %IRI of each prey item (Cortes, 1999), and the trophic level of each prey item was derived from Table 4.2. *Poroderma africanum* had a calculated trophic level of 4.23, and *P. pantherinum* had a calculated trophic level of 4.2.

Despite evidence of an ontogenetic shift in diet, there was a weak shift in trophic levels for both species. The trophic level of *P. africanum* smaller than 85 cm TL was 4.22, while the trophic level individuals larger than 85 cm TL was 4.23. Amongst *P. pantherinum* the trophic level shifted from 4.14 for individuals smaller than 55 cm TL, to 4.19 for individuals larger than 55 cm TL.

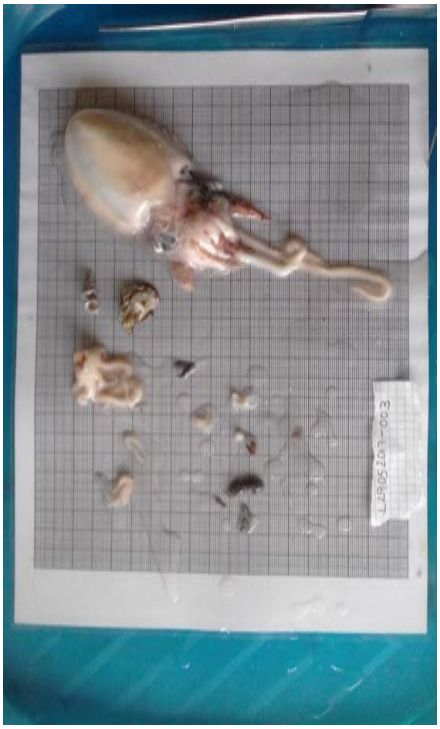
(a) *H. edwardsii* egg cases.

(b) *Hippocampus capensis*.

(c) Juvenile *D. capensis*.

(d) *Callorhinchus capensis*.

(e) *O. vulgaris*.



(f) *Sepia* spp., *O. vulgaris*, and various shell fragments.

Figure 4.9: Selected stomach items of *P. africanum*: (a) to (d); and *P. pantherinum*: (e) and (f).

4.4 Discussion

The stomach content provided insights into the trophic ecology and intra-specific dietary differences between the two *Poroderma* spp. in Mossel Bay and Walker Bay, South Africa. Looking at the overall diversity of food items suggests that *P. africanum* is a generalist carnivore, while the natural diet of *P. pantherinum* consisted almost completely of Cephalopod. The relative low sample size of stomach samples would require the additional collection of the stomach content to further substantiate this. However, as this is the result of a relative low abundance of *P. pantherinum* in the Mossel Bay area (Chapter 3), the increase of the sample size would significantly extend the sampling period, or require alternative (potentially lethal) methods of collecting.

The natural stomach content of *P. africanum* consisted predominantly of a wide variety of Teleost, and, in lower amounts, *O. vulgaris*. While Levin's standardized niche breadth suggested that *P. africanum* is a specialist predator, this was as a result of the number of food groups (Teleost, Cephalopod, Crustacean, Gastropod, etc.) it preyed upon, and not the diversity within those food groups. The wide diversity within the food groups also suggests that *P. africanum* provides a diffused predation risk upon the ichthyofaunal community, by predating a wide diversity of species. This corroborates the diffused predation risk that mesopredators perform on lower trophic level prey (Menge *et al.*, 1994; Heupel *et al.*, 2014).

The natural diet of *P. pantherinum* consisted almost completely of Cephalopod, which was supported by a very low Levin's standardized niche breadth value. The importance of Cephalopod was pronounced in larger individuals, with younger individuals preying on a diversity of species. This indicates that in their natural hunting behaviour both *Poroderma* spp. are active predators, preferring to prey on active swimming fauna. While the sample size was relatively low and the rarefaction curve was not approaching an asymptote, the

results suggest that *P. pantherinum* performs a concentrated predation risk on the cephalopod community (Menge *et al.*, 1994; Heupel *et al.*, 2014). However, the spatial variation in diet suggests this might only be the case in Mossel Bay, as the species shows more of an inclusion of Teleost in their diet in Walker Bay.

The presence of discarded bait in the diet of *P. africanum* suggests that this species can be adaptable to anthropogenic influences and prone to scavenging behaviour as seen in other elasmobranchs (Semeniuk *et al.*, 2009). Mossel Bay has various prolific fishing spots, as well as a commercial harbour, which can serve as possible anthropogenic food sources of discarded fish and by-catch. Many animal species benefit from anthropogenic food sources (e.g., refuse dumps, feeding stations and fishery discards; Oro *et al.*, 2013), such as *Ciconia ciconia* (white storks; Oro *et al.*, 2013), *Canis latrans* (coyotes; Murray *et al.*, 2015), and gulls (Osterback *et al.*, 2015).

Anthropogenic food subsidies can promote changes in life history of many species, potentially increasing population abundances and causing cascading effects through food webs and ecosystems (Robb *et al.*, 2008; Carey *et al.*, 2012; Cortés-Avizanda *et al.*, 2012; Sanz-Aguilar *et al.*, 2015). Reliance on anthropogenic food sources can additionally increase the reliance of species on human activity, altering their natural behaviour and trophic relationships, and impacting their health (Pini-Fitzsimmons *et al.*, 2018).

Both *Poroderma* spp. showed an ontogenetic shift in diet, which correlated to the size at 50% sexual maturity for both species. The diet shift from a teleost-dominated to cephalopod-dominated diet at 85 to 90 cm TL (for both sexes) occurred for *P. africanum* (Table 1.1; Roux, 2002; Dainty, 2002). For *P. pantherinum* the size at 50% sexual maturity ranged from 51 to 67 cm TL for females, and 61 to 77 cm TL for males (Roux, 2002; Mann, 2013), which correlated to a change in size-class from Medium to Large and from Large to Extra-Large, respectively. This means that the

natural diet of *P. pantherinum* shifts towards a cephalopod dominated diet once the species becomes sexually mature. This implies that the adults of this species provides a more concentrated predation pressure on the ecosystem by targeting primarily cephalopods.

Ontogenetic shifts in diet are wide-spread in the animal kingdom (Sánchez-Hernández *et al.*, 2019), and are seen in various fish species, including sharks such as *C. carcharadon* (Hussey *et al.*, 2012b), *G. cuvier* (Lowe *et al.*, 1996) and *Notorynchus cepedianus* (Ebert, 2002). As sharks grow in size, their muscle and jaw development allows for the predation of more sophisticated prey. This has been observed in other species such as *C. carcharias* (Hussey *et al.* 2012b) and *N. cepedianus* (Ebert, 2002). Ontogenetic jaw development might occur with the *Poroderma* spp., and warrants further investigation. However, whether this ontogenetic shift in diet in *P. pantherinum* is due to the more muscular development of the jaws as it grows older, or whether it is due to the increase in overall size of the individual allowing for targeting this specific prey, would require further research.

Poroderma spp. digest cephalopods on average within 22 hours, while teleosts are digested in 42 hours (Dainty, 2002). This implies that the majority of the stomach content in this study was eaten within two days prior of sampling. While cephalopods have a lower energy content (±4.5-5.5 kJ/g) compared with teleost (seabreams: ±6.4-7.4 kJ/g; Spitz *et al.*, 2010), the ratio between the weight to the number of cephalopods consumed (average of 15.1 gr per number) was higher than the average for teleosts (4.1 gr per number). This meant that while cephalopods provided 0.7 times less energy per gram consumed, the total weight consumed was almost 4 times greater than that of teleosts. Furthermore, considering the faster digestion rate, the consumption of cephalopods allows for faster uptake of energy compared with teleosts. This may indicate that the cost of hunting cephalopods outweighs

the cost of hunting teleosts. Further examination into predation costs, whether it is harder to capture cephalopods over teleosts, would need to be required to confirm this.

Examination of the energy content also explains the presence of bait in the stomach content of *P. africanum* across all size-classes. Clupeidae spp. (including *Sardina pilchardus* and *S. sagax*) have a higher energy content than cephalopods and seabreams (±7.5-10.1 kJ/g; Spitz *et al.*, 2010). The ratio between weight and number of bait was also higher than teleost and cephalopods (36.7 gr per number). Thus, the effort-reward paradigm of scavenging for high nutritional food sources provides a greater incentive than preying on natural occurring prey of lower energy content. However, this was only seen in *P. africanum* and not with *P. pantherinum*. Despite occurring in the same area with the same anthropogenic presence, the prominence of cephalopods in the diet of *P. pantherinum*, especially in larger individuals, can suggest a deliberate specialization for this species. On the other hand, *P. pantherinum* is thought to be nocturnal and more active during periods of increased lunar illumination (Chapters 3 and 5; Juby, 2016), and thus their period of activity might not overlap with those times when bait is discarded, but with the activity patterns of their natural prey (Jäckel *et al.*, 2007). As a result, changes in baiting practices would be more likely to strongly impact *P. africanum*, rather than *P. pantherinum*.

Despite the composition of the diet being different between the two species, the trophic levels of the two *Poroderma* spp. were quite similar. No significant change in trophic level was observed between the different life stages of the two species. A review of the literature suggests that the trophic level of elasmobranchs range from 3.1 for *Stegostoma fasciatum* (zebra shark) to 4.82 for *C. carcharias*, with the trophic levels of scyliorhinidae ranging from 3.5 for *Schroederichthys chilensis* (redspotted catshark) to 4.2 for (amongst others) *Halaelurus natalensis* and *H.*

regani (Cortes, 1999; Ebert and Bizzarro, 2007; Bizzarro *et al.*, 2017). The trophic level of *P. africanum* calculated here (TL = 4.23) was higher than determined by Cortes (1999, TL = 3.6), likely due to the higher quantity of teleost and cephalopods and lower quantity of crustaceans found in this study. This higher trophic position indicates that the study species are tertiary consumers. Despite their smaller size, *Poroderma* spp. seem to exert a higher trophic pressure on the ecosystem than initially assumed. As elasmobranchs have a K-selected life history strategy, this could indicate that the species might not be as susceptible to mesopredatory release as a result of a trophic cascade as their initial trophic position might indicate.

Dietary results from this study, in addition to other studies performed in South Africa (Lechanteur and Griffiths, 2003; Dainty, 2002), revealed that the diet of *Poroderma* spp. was not consistent across its distribution. In False Bay the diet of *P. africanum* was made up primarily of crustaceans (%O = 50), with mollusc (%O = 20), polychaetes (%O = 10.2) and teleosts (%O = 15) making up the rest (Lechanteur and Griffiths, 2003). The diet of *P. pantherinum* in False Bay consisted predominantly of teleosts (%O = 31.8), followed by mollusc (%O = 27.3), crustaceans (%O = 18.2) and algae (%O = 4.6; Lechanteur and Griffiths, 2003). Around Gansbaai, the diet of *P. africanum* consisted primarily of teleosts (IRI = 6215), with crustaceans (IRI = 1393) and mollusc (IRI = 986) of lesser importance (Dainty, 2002). The diet of *P. pantherinum* showed similar vertebrate (IRI = 2577) and mollusc (IRI = 2463) content, with a lower crustacean content (IRI = 178; Dainty, 2002). Similar to this study, Dainty (2002) identified *P. africanum* as a generalist predator and *P. pantherinum* as a specialist feeder, with the diet of the latter feeding primarily on molluscs and teleost. The spatial variation displayed in the diet of both *Poroderma* spp., in conjunction with the diversity of prey items, showed that both species are not stenotypic in their diet preferences, and the calculated trophic level can vary depending on where

individuals of the species are sampled. The spatial variation in diet suggests that both species are highly adaptable, however, the diversity in prey items of *P. africanum* could be dependent on the abundance of prey items in respective areas. While the primary identified prey items are present across both sampling areas, further examination in density of prey of the *Poroderma* spp. could elucidate the reason for the spatial variation in diet.

As gastric lavage examines the recently consumed dietary items, further research through the use of stable isotope analysis would be required to determine the long-term diet and overall trophic signatures of the *Poroderma* spp. (Shiffman *et al.*, 2012). However, the influence of artificial food sources (e.g., discarded bait) on the diet of a species has shown to be an influence on the stable-isotope signature in other species (Fisk *et al.*, 2002; Auman *et al.*, 2011; Schurr *et al.*, 2012; Britton and Busst, 2018). Therefore, caution should be taken with the use of stable isotopes in the trophic ecology of the *Poroderma* spp., as inaccurate conclusions may be drawn if the influence of non-native food sources is not taken into account (Petta *et al.*, 2020).

Resource partitioning is one of a few ways to separate species along the trophic ecological axis, and thus avoid competition within benthic fish communities (Scheffer and van Nes, 2006). This could be facilitated by various factors, such as morphological features, foraging behaviour, depth and spatiotemporal variations (Heithaus and Vaudo, 2012). The two *Poroderma* spp. are morphologically similar, with their primary morphological differences being colour pattern and size. While body size is an important variable along the trophic ecological axis (Marti *et al.*, 1993), limited food resources could also be a reason for resource partitioning between the *Poroderma* spp., as seen with the anthropogenic component in the diet of *P. africanum*.

With changing ecosystems due to climate change and overfishing, redistribution of prey can in turn have a strong influence on the survival of predators. Yet a species that has adaptable dietary requirements, is likely to have a higher chance of surviving these changes, and can probably overcome them. While the *Poroderma* spp. show a strong spatial variation in diet, whether these variations can be attributed to the adaptability of the species to changing ecosystems would require further exploration.

Chapter 5

Inter- and Intra-Specific Spatio-Temporal Movement Variation in *Poroderma* spp.

5.1 Introduction

Defining the spatial ecology of marine species is fundamental in understanding how marine ecosystems function (Stocks *et al.*, 2015), as well as their response to environmental and anthropogenic variables (Mucientes *et al.*, 2009). Movement behaviours contributes directly to the type of role a species plays within an ecosystem, which in turn plays an important role in their capability as a species to respond to climate change (Bost *et al.*, 2015; Hazen *et al.*, 2012). Movement also governs animal distributions, and plays an important role in ecosystem functioning (Olds *et al.*, 2012; Espinoza *et al.*, 2015; Abrahms *et al.*, 2017). Various spatial metrices for residency and population structure provide useful information for the management of marine resources (Zeller, 1997; Fromentin and Powers, 2005). Spatial ecology thus plays a central role in conservation ecology and the application to spatial management planning (Fletcher *et al.*, 2011; Espinoza *et al.*, 2015).

Reef-associated species tend to be habitat specialists, depending heavily on reef ecosystems for survival (Roff *et al.*, 2016). These habitats should therefore require all the necessary resources; however, determining how such species gain access and share these resources in these high diversity habitats is complicated (Heupel *et al.*, 2018b). Interactions between reef-associated elasmobranchs are inherently connected to distribution, movement and behaviour patterns of individuals and species (Heupel *et al.*, 2018b). The movement of larger elasmobranchs around reef habitats have been explored in various regions (Papastamatiou *et al.*, 2020; Schlaff *et al.*, 2020; Baremore *et al.*, 2021), with a few studies monitoring multiple species across the same reef system (Espinoza *et al.*, 2015; Lea *et al.*, 2016; Murie *et al.*, 2022; van Zinnicq Bergmann *et al.*, 2022). However, the limited number of studies that examine multiple species across the same habitat, or focus on smaller species such as scyliorhinidae, complicates our understanding on inter-specific dynamics among elasmobranchs and resource-sharing among potential competitors for the same prey (Heupel *et al.*, 2018b). Examination of the movement behaviour of multiple, smaller elasmobranchs in the same area will elucidate the inter-specific dynamics among smaller elasmobranchs and their resource-sharing patterns in reef ecosystems.

Various analyses have been used in the past to explore the movement behaviour of tagged marine animals, such as minimum convex polygons (MCPs) or kernel density estimates (KDEs) (Heupel *et al.*, 2018a). However, the use of these analyses are dependant on the deployment of the array, and these in turn are dependant on what research questions are explored (Heupel *et al.*, 2018a; Mourier *et al.*, 2018). As it is not always feasible to cover the full extent of where the animal moves, strategic placement of the acoustic receivers to examine the movement behaviour would necessitate the use of alternative analyses to understand how species move around the environment. The use of network analysis has gained a lot of traction

in studying animal spatial ecology in recent years (Jacoby and Freeman, 2016; Lea *et al.*, 2016; Heupel *et al.*, 2018b). Also known as graph theory, network theory was first developed for mathematical and social sciences. However, the method is now used across disciplines, such as computational science, physics, management, genetics, and epidemiology (Newman, 2010; Mourier *et al.*, 2018). Network analysis has advanced the understanding of linkages between paired entities, for example habitats, species, individuals, proteins, and genes (Mourier *et al.*, 2018), and has become widely used in ecology. Using a variety of quantitative metrics, network analyses allow for the characterization and analysis of the structure of the network at the node, group, or network level (Mourier *et al.*, 2018).

Limited research has been done on the movement behaviour of the *Poroderma* spp. previously. Escobar-Porras (2009) conducted a preliminary study into the residency of *Poroderma* spp. using passive acoustic telemetry in the Tsitsikamma Marine Protected Area, however, the use of acoustic telemetry in that study was limited to the presence/absence of five *P. pantherinum* in two small embayments.

As movement behaviour is an essential component in understanding how two sympatric species co-occur within the same area, the aim of this chapter is to examine inter- and intra-specific variation in movement behaviour between *P. africanum* and *P. pantherinum*. To determine whether movement behaviour is consistent throughout their distribution, mark-recapture data from conventional tagging data for both species throughout South Africa is examined. This is followed by the examination of space use within the Mossel Bay area using passive acoustic telemetry. By examining the use of space and depth the underlying patterns were explored and correlated to environmental variables. The primary research questions of this chapter were:

- Are there differences in residency and broad-scale movement behaviour between *P. africanum* and *P. pantherinum* across their distribution?
- Are there differences in residency and space use between two reef-associated

species within a small embayment?

- Is there temporal variation in space use between two reef-associated, sympatric elasmobranchs?

5.2 Methods

The movement patterns of the two *Poroderma* spp. in Mossel Bay were assessed using data collected from mark-recapture dart tagging and passive acoustic telemetry.

5.2.1 Mark-Recapture

Between 1984 and 2018, *Poroderma* spp. caught with conventional fishing tackle were tagged with a dart-tag (Hallprint©; Hindmarsh Valley, Australia) as part of the Oceanographic Research Institute-Cooperative Fish Tagging Project (ORI-CFTP; see Dunlop *et al.*, 2013 for details). During the tagging and recapture procedure, anglers recorded the date, the unique tag number, species, length (Pre-Caudal Length (PCL) or Total Lenght (TL), in cm), and sex. For individuals that were recaptured, the recapture location was linked to the original tagging location (Dunlop *et al.*, 2013). This dataset was provided by ORI in Durban, South Africa.

5.2.2 Passive Acoustic Telemetry

5.2.2.1 ATAP Receiver Array

Mossel Bay has a history of past movement behaviour studies (Johnson *et al.*, 2009; Delaney *et al.*, 2015; Jewell *et al.*, 2013; Gennari *et al.*, 2022), and hosts a passive acoustic receiver array (models VR2W and VR2AR, Innovasea, Halifax, Canada) under the auspices of the Acoustic Tracking Array Platform (ATAP; Cowley *et al.*,

2017). The existing ATAP receiver array in Mossel Bay was complemented with five additional receivers for this study (Figure 5.1).

The receivers were deployed in series of one-dimensional arrangements, so-called "curtains". A three-receiver curtain was deployed off the Mossel Bay peninsula. A seven-receiver curtain was deployed approximately 10 kilometres away from Mossel Bay, near the Klein Brak Estuary. The last three-receiver curtain was deployed another 5 km further east near the Groot Brak River Estuary (Figure 5.1).

5.2.2.2 Range Test & Receiver Deployment

Range tests were performed to determine whether, depending on where the receiver would be placed, an acoustically tagged animal would be able to be detected on the reef. The range tests were designed so that two transmitters (V16-4H), identical to those to be inserted into the animals to ensure no variability in detection would occur as a result of technical differences, were attached to a weighted (floating) rope. As both *Poroderma* spp. are considered to be benthic and are usually seen by local divers swimming close to the reef substrate, one transmitter was placed near the sea floor, and one 1 m above the weight. The transmitters were deployed in a central location of a reef, and their signal was measured using an Innovasea VR100 receiver (at 48 gain) in three orthogonal directions in 100 m increments from the transmitters, up to 1000 m or until both transmitters were no longer detected. Two transects were performed parallel to the coast, while the third direction was performed perpendicular to the coastline. An omnidirectional hydrophone was used, and to simulate the position of the VR2W hydrophone receiver, the hydrophone was lowered as close to the bottom as possible. Comparison between a VR100 and a fixed receiver (VR2W) indicated that the fixed receiver had a higher detection quality of the acoustic transmitters after 200 m (Singh *et al.*, 2009), thus confirmation of the detection of both transmitters on the VR100 would have a higher probability of being detected when compared to a VR2W

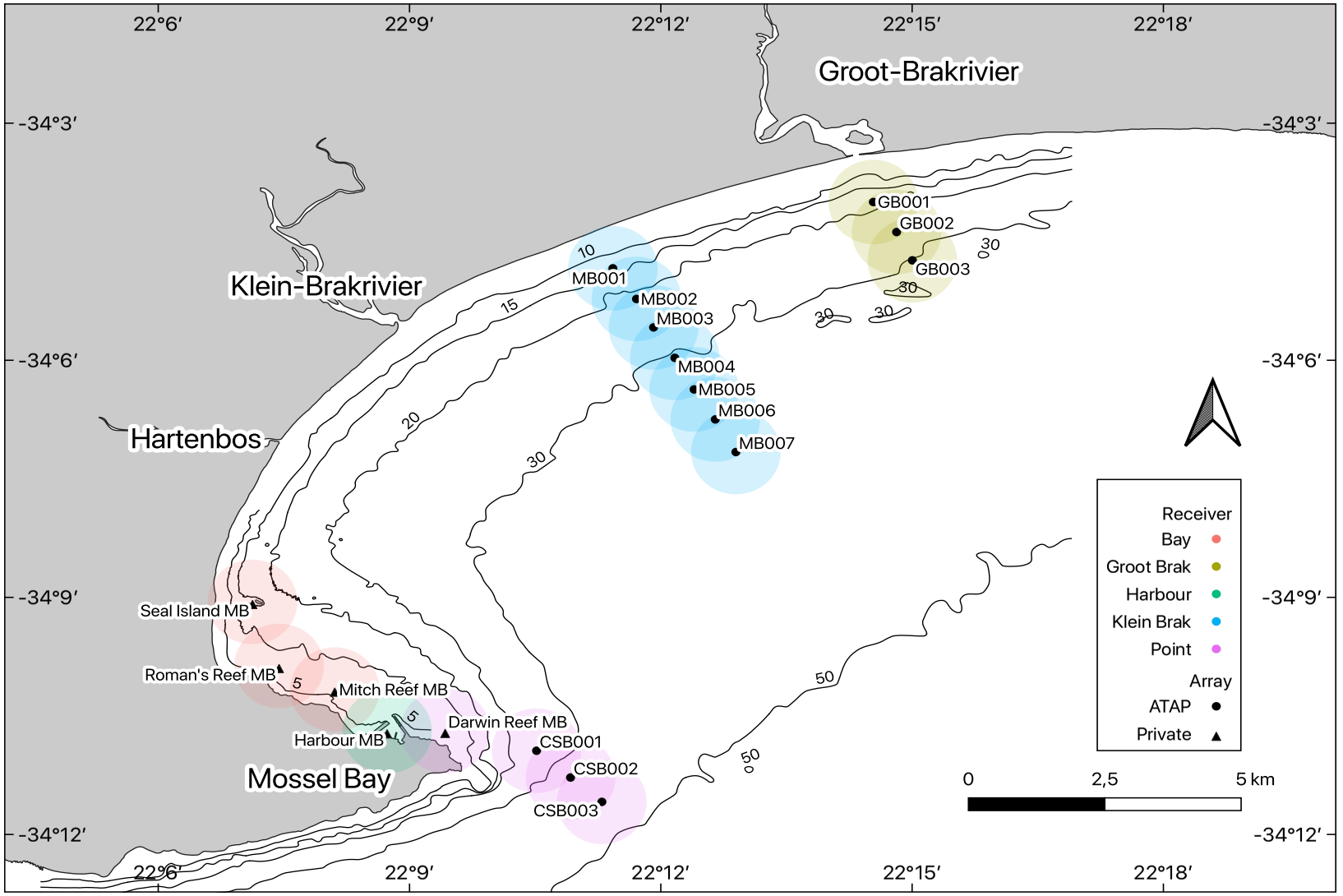


Figure 5.1: Map of receiver locations in Mossel Bay, showing the five clusters used for Continuous Residency Time calculations, and the private (Oceans Research) and national (ATAP) receiver arrays. Created with qGIS v3.12.

The range tests indicated an average detection range of 867 ± 231 m (mean ± sd; Roman's Reef) and 833 ± 208 m (Mitch Reef).

The design of the moorings for these additional inshore receivers was based on previous moorings deployed in the Mossel Bay area (Delaney *et al.*, 2015). The moorings were concrete filled tires with a steel I-beam inserted, angled perpendicular to the sea floor, and secured with an additional cross-welded I-beam for security. The receiver was attached at the top of the main I-beam, approximately 1 m from the sea floor. The receiver was attached so the hydrophone stuck out above the I-beam and was thus unobstructed by the steel bar.

Following the range test, three receivers were strategically placed perpendicular to the coastline, to ensure that one receiver was associated with, and acoustically covering, at least a single reef. Placing the receiver on top of the reef would drastically decrease the detection range due to the reef structure, increased sound pollution due to wave action as a result of the shallow depth, and increase the chances of human interference.

Two receivers were placed approximately 200 m from Roman's and Mitch Reef, respectively, and approximately 150 m from Darwin Reef, well within the range of the acoustic receiver to pick up tagged animals on the reef and to account for any variability caused by incremental weather (Figure 5.2; final receiver deployment location were indicated with red triangles). The range test indicated possible overlap in detections between Roman's and Mitch Reef receivers, these double detections were removed during the data cleaning stage to present the most accurate movement possible.

One receiver was deployed on the west side of Seal Island, away from the area where a pilot study identified >90% of *Arctocephalus pusillus pusillus* departed the island from (Morse *et al.*, 2019; R. Johnson unpublished data). The last receiver was deployed within the harbour, as this might be a possible anthropogenic source of

food; near the recreational yacht jetty (Figure 5.1).

5.2.2.3 Receiver Soak Time

Eighteen receivers were deployed between August 2015 to March 2018 for a cumulative total of 16459 days.The data from three receivers (Darwin Reef MB, Roman's Reef MB, Mitch Reef MB) were not recovered between October 2016 and October 2017 due to equipment loss, while Seal Island MB was not changed over in this time due to hazardous conditions surrounding its deployment.

5.2.3 Data Analysis

5.2.3.1 Mark-Recapture

Conventional mark-recapture provided an understanding of the site fidelity and travel distance for both species, by looking at the duration between mark and recapture times, and the distance travelled from the initial tagging site. The mark-recapture data allowed the following metrices to be calculated: Time at liberty (days), distance moved between release and recapture sites (km), and the minimum rate of movement (km/day). The Total Length (mm) were provided by ORI. To determine whether the movement was consistent throughout their distribution, movement between capture and recapture localities of the *Poroderma* spp. were visualized on a map of South Africa. Movement patterns were explored roughly along a west-east direction.

Wilcox sum-rank tests were used to compare the distance travelled, time at liberty, and the minimum rate of movement between species, and linear regressions were performed to correlate the size of the individual animals to the distance travelled.

Movement behaviour through mark-recapture was closer examined within Mossel Bay, the study site.

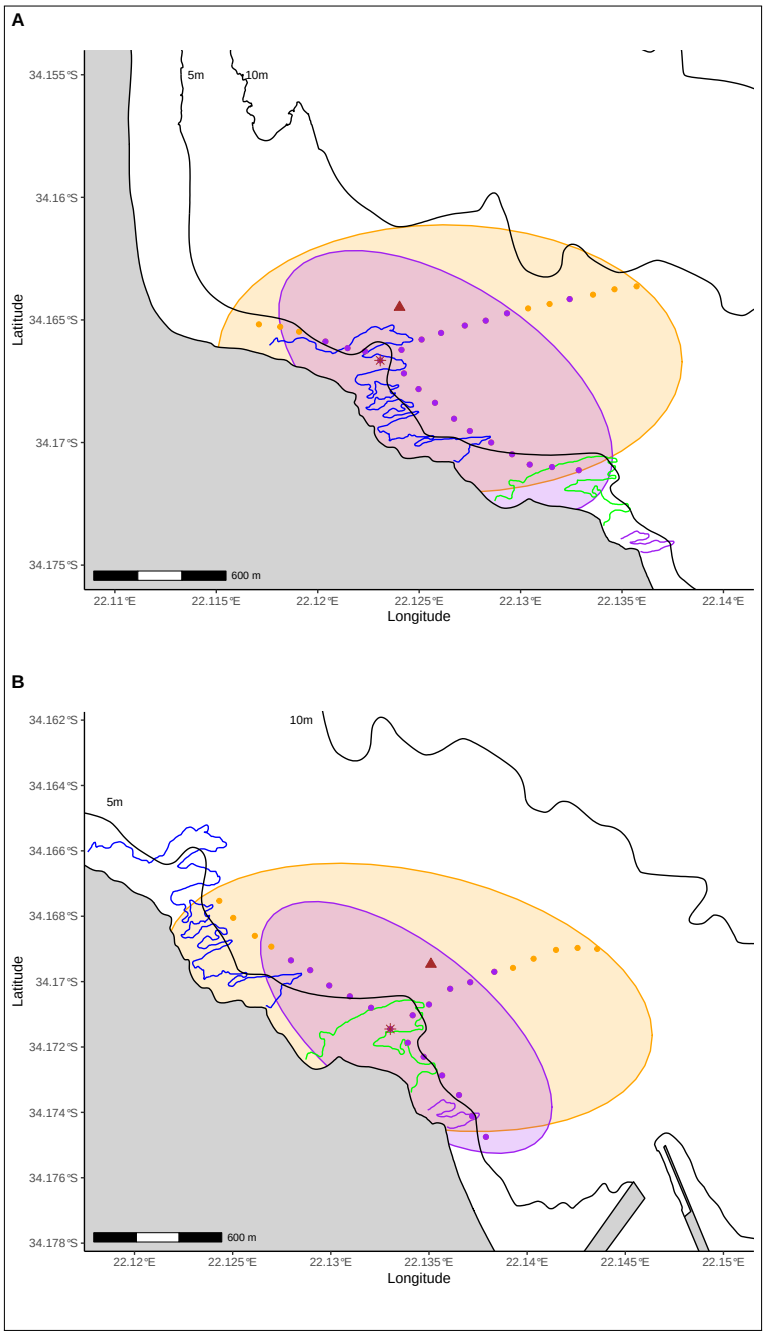


Figure 5.2: Range test results at (A) Roman's (blue) and (B) Mitch Reef (green): Purple shows the detection of both test transmitters, orange shows the detection of only one transmitter. The ellipses were generated assuming a multivariate t-distribution. The star indicates the deployment location of the test transmitters, and the triangle indicates the final deployment of the receiver associated with that reef. Created with R v3.6.2.

5.2.3.2 Passive Acoustic Telemetry Data

The data downloaded from the acoustic receiver was cleaned prior to further analysis. Single detections within 24 h on a single receiver were removed. Non-sensical detections, i.e., subsequent detections that made no ecological sense, were removed as well. Detections that overlapped on multiple receivers were filtered to represent the most accurate movement from one receiver to another. This was generally performed through the removal of detections from either side of the adjacent receivers until a smooth transition was shown from one receiver to another.

5.2.3.3 Residency

Two forms of residency, Continuous Residence Time (CRT) and Residency Index (RI), and a Roaming Index (ROI) were calculated.

Continuous Residence Time (CRT) as defined by Ohta and Kakuma (2005), is the duration within which a tagged fish was continuously monitored at a specific location without day-scale ($>$ 24 h) absences. CRT was used to determine how long individuals of both species resided in different locations of the study area. For the determination of the CRT, the acoustic array was divided into five separate locations. They were grouped according to adjacency, and separated if there were any large physical objects separating the two adjacent receivers (i.e harbour walls). The receiver curtains at Klein Brak and Groot Brak were grouped into "KB" and "GB", respectively, due to their distinct geographical distance. The acoustic receivers near Roman's Reef, Mitch Reef and Seal Island were grouped into inshore (shallow) sheltered bay ("Bay"), while the acoustic receiver near Darwin Reef was grouped with the CSB receiver curtain into inshore exposed coast ("Point"). Due to its separation from the rest of the array by the harbour walls, the acoustic receiver within the Mossel Bay harbour was grouped by itself (Figure 5.1).

To account for the day scale, a maximum blanking period (MBP) was assigned. The MBP is the maximum amount of time allowed between two subsequent acoustic detections for considering that a tagged individual is still present at a particular location. The CRT is thus defined as time units where the temporal separation between subsequent acoustic detections is smaller than the MBP, unless the individual is detected in another location, at which point another CRT is started anew (Capello *et al.*, 2015). As *Poroderma* spp. are known to occupy rocky reefs, have unknown activity patterns, and limited knowledge surrounding the species' ranging habits, two MBPs were assigned: one of 24 hours, and one of 48 hours. The R-script for calculating the CRT values was obtained from Rodriguez-Tress *et al.*, 2017. (URL: `www.int-res.com/articles/suppl/m570p213_supp2.zip`).

Residency Index (RI) was used to determine how long each individual per species was resident at various receivers and throughout the array. The RI for each individual (i) at each receiver (j) was calculated using Equation 5.2.1.

$$RI_{ij} = \frac{(\text{Days Detected})_{ij}}{(\text{Days Monitored})_{j}} \qquad \text{(eq. 5.2.1)}$$

Days Monitored was considered to be the number of days the receiver was deployed, from the day an individual was tagged, until the 26 March 2018, the last day the Seal Island, Roman's Reef, Mitch Reef, Harbour and Darwin Reef receivers were retrieved. Values ranged from 0 to 1, with high values representing high levels of residency and vice-versa. A Wilcoxon-rank sum test was performed to determine whether residency differed significantly between the two *Poroderma* spp.

Roaming Index (ROI) was calculated to identify the dispersion of individuals throughout the array, which was calculated as the number of receivers an individual was detected on, divided by the total number of receivers (n = 18;

Heupel *et al.*, 2018b). RI and ROI were plotted against each other to visualise species-specific patterns. Both RI and ROI were arcsine transformed and compared between species using MANOVA, with species as the factor (O'Brien and Kaiser, 1985).

The number of days the two species were detected together on the same receiver were isolated, and compared to the number of days the receivers were active.

To determine transmitter attrition in the study area, survival curves were generated. Transmitter attrition can be caused by: (i) faulty transmitter, (ii) dispersal, or (iii) mortality (Afonso *et al.*, 2012). The individual was considered still to be present in the study area if the last detection was within the last three months of the study.

5.2.3.4 Abiotic Data

To test whether there was any correlation between environmental data and movement behaviour, weather data were collected during this study. Daily satellite Sea-Surface Temperature data was collected via NOAA's online dataset (URL: `https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST.html`; resolution: 0.011°). Humidity, rain, wind speed and direction were provided by the South African Weather Service (SAWS). Tidal data were provided by the South African Navy Hydrographer Office, while lunar data was collected from `www.vercalendario.info`.

5.2.3.5 Fine-scale rhythmic patterns

To determine whether there was any diel temporal pattern for the two *Poroderma* spp., proportions of hourly detections were used. The first detection per hour per day per individual were selected to avoid high numbers of detections if animals were detected at the same receiver for extended periods, and thus to minimize the

possibility of receiver detection efficiency influencing the analyses. The detections were subsequently summed per hour per individual, and chi-square tests were used to determine whether the detections over 24 hours differed from an even distribution. A subsequent PERMANOVA (using `vegan`'s `adonis`-function in `R`; Oksanen *et al.*, 2013) was used to determine whether species, sex, or size influenced the utilization of the array over a 24h cycle.

To determine whether the detections had any underlying rhythm, spectral analysis using a Fast Fourier Transform (FFT) was performed. This analysis can detect rhythms in the time series, allowing a periodic character to be visualized in a power spectrum (Chatfield, 2004). The FFT was conducted on each species to compare overall species variations, and individuals of each species to explore individual variations.

Daily temporal excursion patterns were explored by combining both the departure times from one receiver to another, and individuals that were not detected at a receiver for more than 24 hours (assuming they left the area of receiver detection), into 10-minute bins over 24 hours. To test whether the detection data were evenly distributed over 24-hour periods, Rao Spacing tests (Batschelet, 1981) were performed. Differences within species and sex were tested using Wilcox-sum-rank tests (due to non-normally distributed data), and within species between months using a Kruskal-Wallis Rank sum test (Hollander *et al.*, 2013).

5.2.3.6 Spatial Connectivity and Depth Use

The movement patterns of *Poroderma* spp. were assessed using network analysis. Networks were generated using R's `igraph`-package (Csardi and Nepusz, 2006). The network was fixed into place with the nodes representing the individual receivers. The nodes were weighted according to the average RI per species, while the weight of the edges, representing the movement between the receivers, were determined

according to the total number of transects between the respective receivers for each species.

Excluding fine-scale movement within and outside receiver ranges, the individual distance travelled between receivers was calculated by multiplying the number of transects between receivers by the distance between those receivers.

A generalized linear model was constructed for each species to correlate the depth of the receiver to the RI of individually tagged animals.

To determine the extent of movement within the receiver network, Edge Density (ED), the ratio of the number of edges and the total number of possible edges in the network, a number between 0 and 1, was calculated (Mourier *et al.*, 2018). Betweenness was calculated to determine which receivers were important for spatial connectivity, with higher values indicating high importance and low values the opposite (Mourier *et al.*, 2018). A Clustering Coefficient (CC) was calculated (Wasserman and Faust, 1994) to determine the tendency that one receiver was connected to other well-connected receivers (Mourier *et al.*, 2018), generating a number from 0 to 1. The Eigenvector Centrality (EC) was calculated by the sum of all incoming and outgoing movements from the receiver, weighted by the strength of the adjacent receivers (number of receivers that a receiver is connected to). Receivers with a high EC value had high receiver strength values and are connected to receivers with similarly high receiver strength values.

5.3 Results

5.3.1 Mark-Recapture

A total of 2437 individuals of the *Poroderma* spp. were tagged with dart tags between the 29 July 1984 and 4 October 2018. Six of these were tagged in Namibia (all supposed *P. pantherinum*) far outside of the species range, and 13 (12 *P. africanum* and 1 *P. pantherinum*) had unknown capture localities. These were omitted from

the dataset.

Of the remaining 2418 individuals that were tagged in South Africa (1613 *P. africanum*, 805 *P. pantherinum*), 235 individuals were tagged between St. Helena Bay in the Western Cape and St Lucia in KwaZulu-Natal and recaptured between Groot Springfontein in the Western Cape and Dwesa Point in the Eastern Cape.

The majority of both species were recaptured at the exact same location as their initial tagging location (76.3% and 76.9% for *P. africanum* and *P. pantherinum*, respectively). Of the recaptured individuals, only 4.6% of *P. africanum* and 5.8% of *P. pantherinum* were recaptured further than 20 km from their first tagging site (Figure 5.3). Only three *P. africanum* and three *P. pantherinum* individuals travelled further than 100 km (2.3% and 3.1%, respectively). The furthest distance travelled for *P. africanum* was 381 km, from Storms River (Eastern Cape) on 16 August 2003 to Lekkerwater (Western Cape) on 6 November 2003. The furthest distance travelled for *P. pantherinum* was 722 km, from Holbaai Point (Western Cape) on 18 May 1985 to St. Francis Bay (Eastern Cape) on 4 December 1988 (Figure 5.4A).

Time at liberty for *P. africanum* ranged from 0 days to 3074 days (8.4 years), with an average of 411.88 days (1.1 years) ± 566.51 days (mean ± sd). For *P. pantherinum* time at liberty ranged from 0 days to 3139 days (8.6 years), with an average of 342.46 days (0.9 years) ± 450.5 days (Figure 5.5).

Minimum movement speed was calculated based on the distance between release and capture site and the time at liberty in km/day. These ranged for *P. africanum* from 0 to 4.65 km/day (0.05 km/day ± 0.41 km/day; mean ± sd). For *P. pantherinum* the movement speed ranged from 0 to 0.56 km/day (0.04 km/day ± 0.12 km/day).

There were no significant differences between the two species in the distance travelled (W = 6794, p = 0.964), time at liberty (W = 6509, p = 0.773), nor minimum movement speeds (W = 6573, p = 0.827). There was also no significant correlation between the size of the individuals and distance travelled (*P. africanum*:

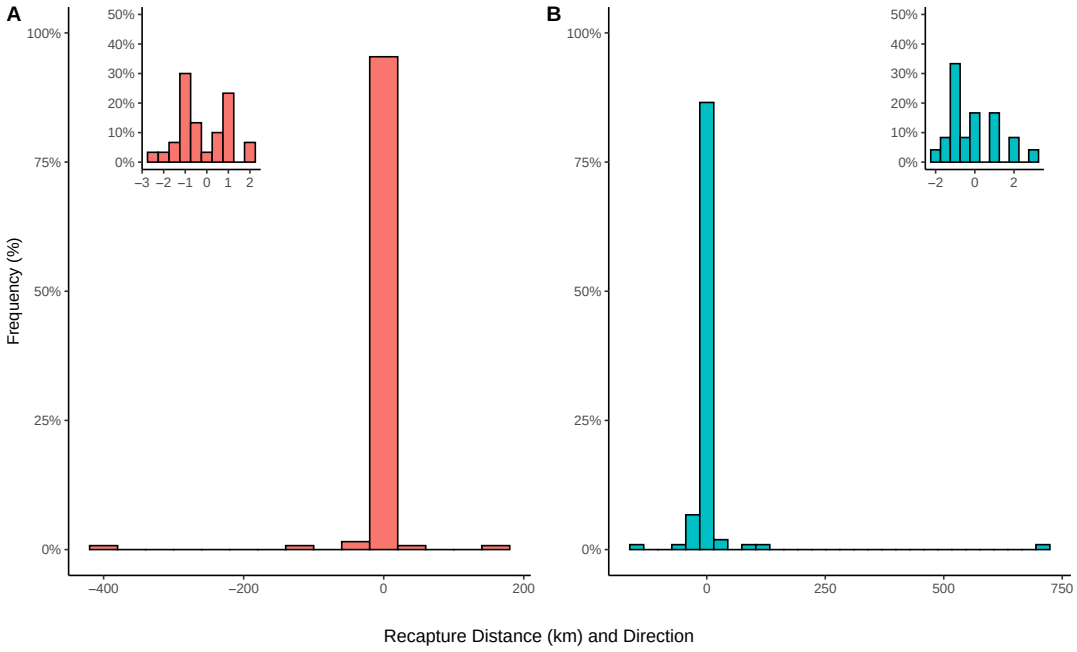


Figure 5.3: Proportion of dart-tagged recaptures of (A) *P. africanum* and (B) *P. pantherinum* at various distances and directions (with west being negative, and east being positive) from their original tagging site. Insets: recaptures with log-transformed distances.

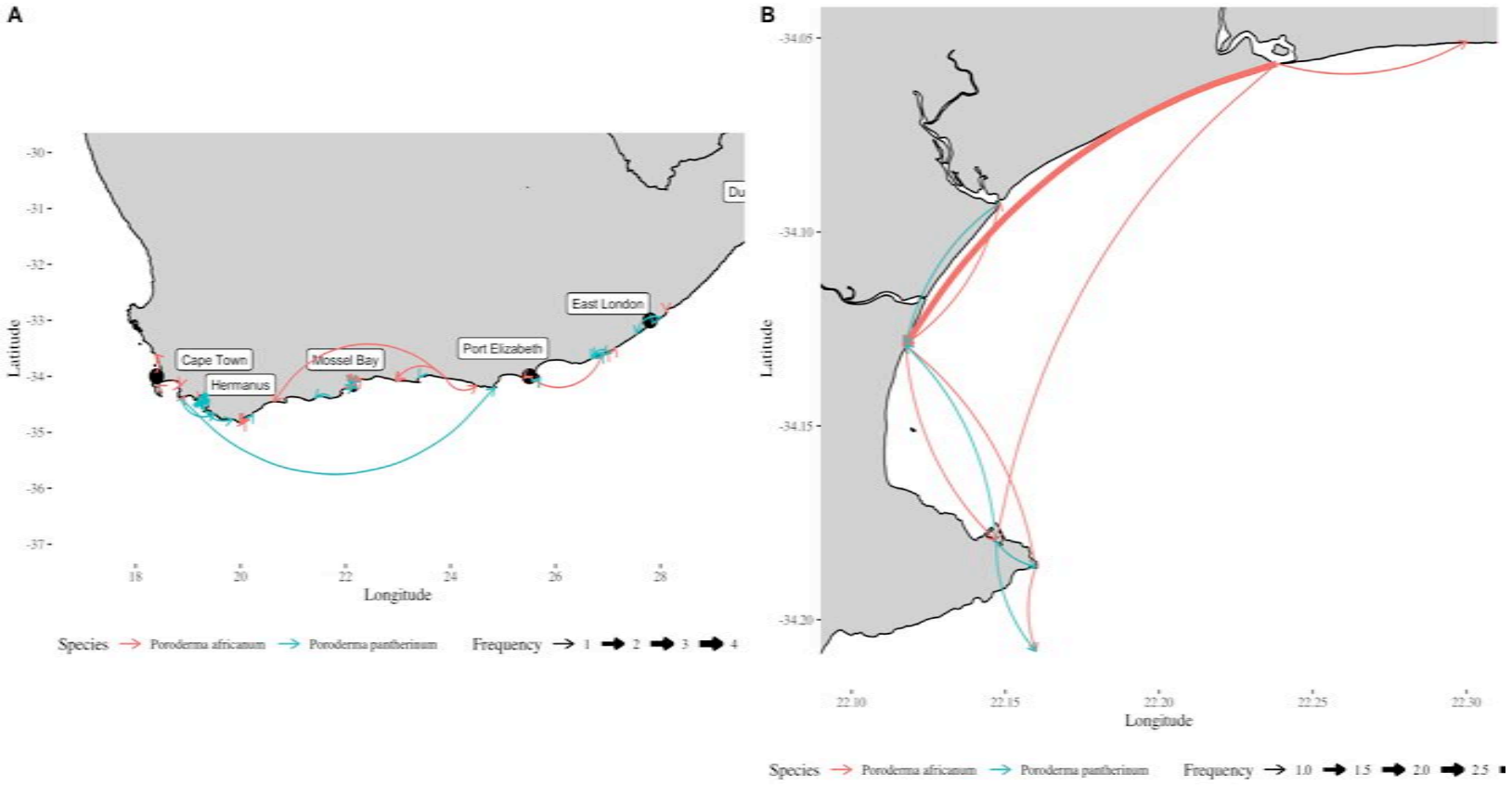


Figure 5.4: Movement of tagged and recaptured *P. africanum* and *P. pantherinum* in (A) South Africa and (B) Mossel Bay between 1984 and 2018, with width of the arrows indicating the frequency of capture and release of individuals between two points. Created with R v3.6.2.

F[2 , 128] = 1.24 , p = 0.267; *P. pantherinum*: F[2 , 102] = 0.29, p = 0.594).

The high degree of site fidelity by both species was also observed in the primary study site, Mossel Bay. Within Mossel Bay, a total of 496 *P. africanum* and 169 *P. pantherinum* were tagged between 1984 and 2018. This resulted in 53 (10.7%) and 22 (13%) recaptures for *P. africanum* and *P, pantherinum*, respectively. Of the recaptures, 11 *P. africanum* and 4 *P. pantherinum* were recaptured away from their initial tagging location, moving up to a maximum of 21 km and 7 km, respectively (Figure 5.4B).

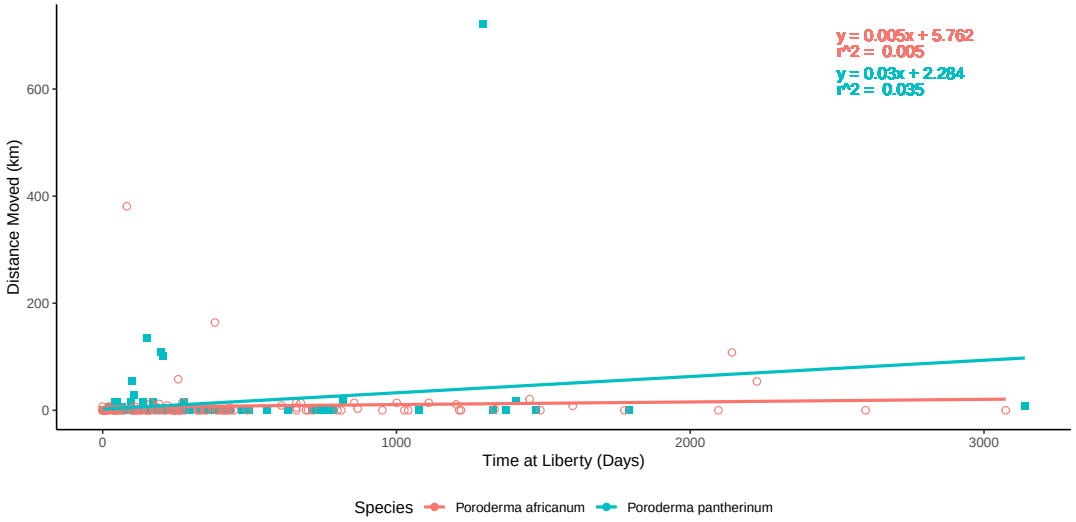


Figure 5.5: Plot of time at liberty in days against distance moved in km for *P. africanum* (red) and *P. pantherinum* (blue), with linear regression formulas and r^2.

5.3.2 Passive Acoustic Telemetry

A total of 21 catsharks were tagged with acoustic transmitters during this study: 11 *P. africanum* (six males and five females) and ten *P. pantherinum* (four males and six females; Table 5.1).

The tag to weight ratio for *P. africanum* did not exceed the 1.25% in water rule of thumb (Winter, 1996). The mean length of tagged *P. africanum* was 88.73 ± 6.41 cm (mean ± sd), with no significant difference between the two sexes (mean female:

86.90 cm; mean male: 90.26; t = -0.86, df = 8.85 p = 0.414). Four *P. africanum* were tagged on Darwin and Roman's Reef each, while three were tagged at Mitch Reef (Table 5.1). The lengths of the tagged *P. africanum* were converted to weight using Equation 5.3.1:

$$W = 0.00674 * TL^{2.958} \quad \text{(eq. 5.3.1)}$$

with weight (W) in gr and Total Length (TL) in cm.

This was compared to the weight of the tag in water. The tag to weight ratio for *P. africanum* ranged from 0.19% to 0.37% (mean ± sd: 0.27 ± 0.06%).

The tag to weight ratio for *P. pantherinum* did not exceed the 1.25% in water rule of thumb. The average length at tagging of *P. pantherinum* was 60.4 ± 4 cm, with no significant differences between the two sexes (mean female: 61.0 cm; mean male: 59.5 cm; t = 0.51, df = 4.84 p = 0.632). Five *P. pantherinum* were tagged at Roman's Reef, while three were tagged at Darwin Reef, and two at Mitch Reef (Table 5.1). The lengths of tagged *P. pantherinum* were converted to weight using Equation 5.3.2:

$$W = 0.00802 * TL^{2.92} \quad \text{(eq. 5.3.2)}$$

with weight (W) in gr and Total Length (TL) in cm.

This was compared to the weight of the tag in water. The tag to weight ratio for *P. pantherinum* ranged from 0.62% to 1.15% (mean ± sd: 0.83 ± 0.17%).

5.3.2.1 Residency

Ten of the eleven tagged *P. africanum* and nine of the ten *P. pantherinum* were detected during the study. Of the 11 *P. africanum* tagged, 10 were detected during the study. Of the 10 *P. pantherinum* tagged, nine were detected. Subsequent analyses were performed on these nineteen tagged individuals. *Poroderma africanum* was

Table 5.1: Summary table of acoustically tagged *Poroderma* spp. All *Poroderma* individuals were tagged with V16-4H (VEMCO) acoustic transmitters.

Tag #	**Species**	**Sex**	**Tag Location**	**Tag Date**	**TL (cm)**
25862	*Poroderma africanum*	Female	Roman's Reef	2015-10-07	79.0
25863	*Poroderma africanum*	Male	Mitch Reef	2015-10-29	84.5
25864	*Poroderma africanum*	Male	Roman's Reef	2015-11-10	93.5
25865	*Poroderma africanum*	Male	Roman's Reef	2015-11-10	83.5
25866	*Poroderma africanum*	Female	Darwin Reef	2015-11-11	91.0
25867	*Poroderma africanum*	Female	Darwin Reef	2015-11-11	93.0
25869	*Poroderma africanum*	Male	Darwin Reef	2015-11-11	100.0
25870	*Poroderma africanum*	Male	Darwin Reef	2015-11-11	94.5
25875	*Poroderma africanum*	Female	Mitch Reef	2016-05-11	81.5
25880	*Poroderma africanum*	Male	Roman's Reef	2016-05-13	85.5
23633b	*Poroderma africanum*	Female	Mitch Reef	2017-01-19	90.0
25868	*Poroderma pantherinum*	Male	Roman's Reef	2016-04-12	66.0
25871	*Poroderma pantherinum*	Male	Roman's Reef	2016-05-05	58.5
25873	*Poroderma pantherinum*	Male	Roman's Reef	2016-05-10	53.5
25874	*Poroderma pantherinum*	Female	Darwin Reef	2016-05-10	63.5
25879	*Poroderma pantherinum*	Female	Darwin Reef	2016-05-12	62.0
25881	*Poroderma pantherinum*	Female	Mitch Reef	2016-05-13	59.0
25882	*Poroderma pantherinum*	Female	Mitch Reef	2016-05-16	62.0
25883	*Poroderma pantherinum*	Male	Darwin Reef	2016-05-23	60.0
25884	*Poroderma pantherinum*	Female	Roman's Reef	2016-06-07	55.0
23639	*Poroderma pantherinum*	Female	Roman's Reef	2017-03-23	64.5

detected on average 161.6 days (95% CI:70.6–252.6), while *P. pantherinum* was detected on average 126.22 days (95% CI:76.5–175.9). An abacus plot of the CRT periods showed that both species were detected more frequently in the first year of the study compared to the following years (Figure 5.6).

On average the two species were detected on the same receiver on the same day during 350 occasions (2.13%) over the entire array. The majority of the co-detections occurred on Roman's Reef with 169 occasions (26.91%), at Mitch Reef with 71 occasions (11.31%), at Darwin Reef with 50 occasions (8.04%), and at acoustic receiver CSB001 with 48 occasions (4.85%; Table 5.2). There were no occasions of the two species being detected on the same day on any of the Klein Brak (MB001–7) or Groot Brak (GSB001–3) receiver arrays, nor at CSB003 or the Harbour receiver.

Table 5.2: Number of days acoustically tagged *P. africanum* and *P. pantherinum* were detected on each acoustic receiver and number of days they were detected on the same day (in count and percentage), with the number of days the receiver were active.

Station	**Days Active**	***P. africanum* Days Detected**	***P. pantherinum* Days Detected**	**Days Co-detected**	**Co-detected (%)**
Roman's Reef MB	628	330	700	169	26.91
Mitch Reef MB	628	156	94	71	11.31
Darwin Reef MB	622	130	126	50	8.04
CSB001	990	433	109	48	4.85
CSB002	990	90	41	8	0.81
Seal Island MB	687	158	7	4	0.58
MB003	990	5	3	0	0.00
MB004	990	2	25	0	0.00
MB005	990	2	2	0	0.00
MB002	990	37	5	0	0.00
MB001	990	169	16	0	0.00
GB001	990	7	4	0	0.00
GB002	990	23	3	0	0.00
MB006	990	4	0	0	0.00
MB007	990	5	0	0	0.00
GB003	990	15	0	0	0.00
Harbour MB	990	37	1	0	0.00
CSB003	990	12	0	0	0.00

The Continuous Residency Time (CRT) set to a minimum blanking period of

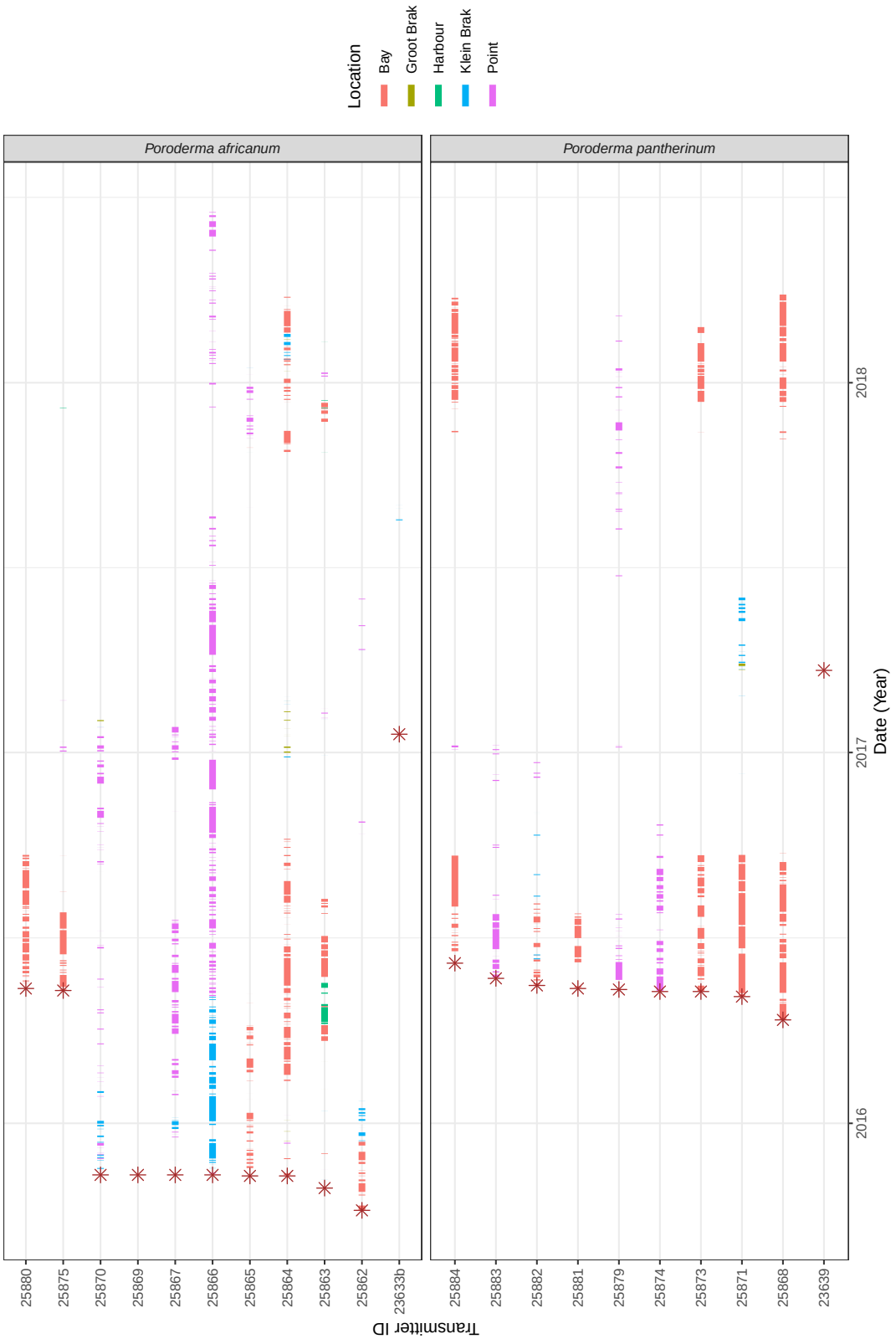


Figure 5.6: CRT periods of tagged *Poroderma* spp. at the various locations around Mossel Bay, South Africa, with the brown star representing the tagging date of the individual.

24 hours (CRT_{24}) indicated that *P. africanum* was resident at a receiver group (Figure 5.1) for an average of 2.01 days (95% CI: 1.66–2.36 days). A female *P. africanum* (ID25866) had the highest CRT_{24} of 29.52 days at the Point.

Expanding the minimum blanking period to 48 hours (CRT_{48}), *P. africanum* was resident in an area for an average of 3.4 days (95% CI: 2.68–4.13 days), with a maximum CRT_{48} of 50.49 days (again by ID25866 at the Point).

The CRT_{24} for *P. pantherinum* was significantly higher than *P. africanum* (W = 68839, $p < 0.05$), with an average residency in an area of 3.32 days (95% CI: 2.53–4.11 days), and a maximum CRT_{24} of 50.31 days by ID25884 within the Bay.

Expanding the minimum blanking period to 48 hours, the average residency within an area increased to 6.42 days (95% CI: 4.28–8.56 days), with a maximum CRT_{48} of 94.18 days by ID25871 within the Bay, which was also significantly higher than *P. africanum* (W = 31204, $p < 0.01$).

Isolating the harbour as a possible anthropogenic source of food showed that only four individuals were detected on the Harbour receiver. Of these, three were detected on single occasions (n = 1). However, ID25863 was detected on 13 occasions (8183 detections), with a maximum CRT_{24} of 14.69 days.

Female *P. africanum* were significantly more resident than the males for both minimum blanking periods (CRT_{24}: W = 37452.5, $p < 0.001$; CRT_{48}: W = 18961, $p < 0.001$). Females had an average CRT_{24} of 2.44 days (95% CI: 1.82–3.06 days) compared to males with 1.67 days (95% CI: 1.27–2.07 days), and an average CRT_{48} of 4.11 days (95% CI: 2.92–5.29 days) for females, compared to 2.88 days (95% CI: 1.97–3.78 days) days for males.

Similarly, female *P. pantherinum* were significantly more resident than male *P. pantherinum* for both minimum blanking periods (CRT_{24}: W = 5778.5, $p < 0.001$; CRT_{48}: W = 2469, $p = 0.161$). Female *P. pantherinum* had an average CRT_{24} of 2.2 days (95% CI: 1.33–3.07 days) compared to 4.75 days (95% CI: 3.36–6.14 days) for males, and an average CRT_{48} of 4.33 days (95% CI: 2.22–6.45 days) for females

compared to 9.31 days (95% CI: 5.15–13.48 days) for males.

Individual RI ranged from 0.005–0.174 for *P. africanum*, with an average of 0.04 and 95% CI from 0 to 0.08 (Figure 5.7A). The individual RI for *P. pantherinum* ranged from 0.017–0.079, with an average of 0.04 and 95% CI from 0.03 to 0.06.

Individual ROI ranged from 0.111–0.889 for *P. africanum*, with an average of 0.43 and 95% CI from 0.24 to 0.61, while for *P. pantherinum* the individual ROI ranged from 0.111–0.389, with an average of 0.23 and 95% CI from 0.17 to 0.3.

There was inter- and intra-specific variation in both RI and ROI, with *P. pantherinum* showing more of a grouping compared to *P. africanum*, which showed a wider spread of ROI (Figure 5.7A). However, no significant differences in RI and ROI between species were present (MANOVA: $F_{1,17} = 2.01$, $p = 0.167$; Table 5.3). There was no signifcant correlation between ROI and the size of the individual for either species (*P. africanum*: $F = 0.02$, $p = 0.898$; *P. pantherinum*: $F = 0.08$, $p = 0.791$; Figure 5.7B)

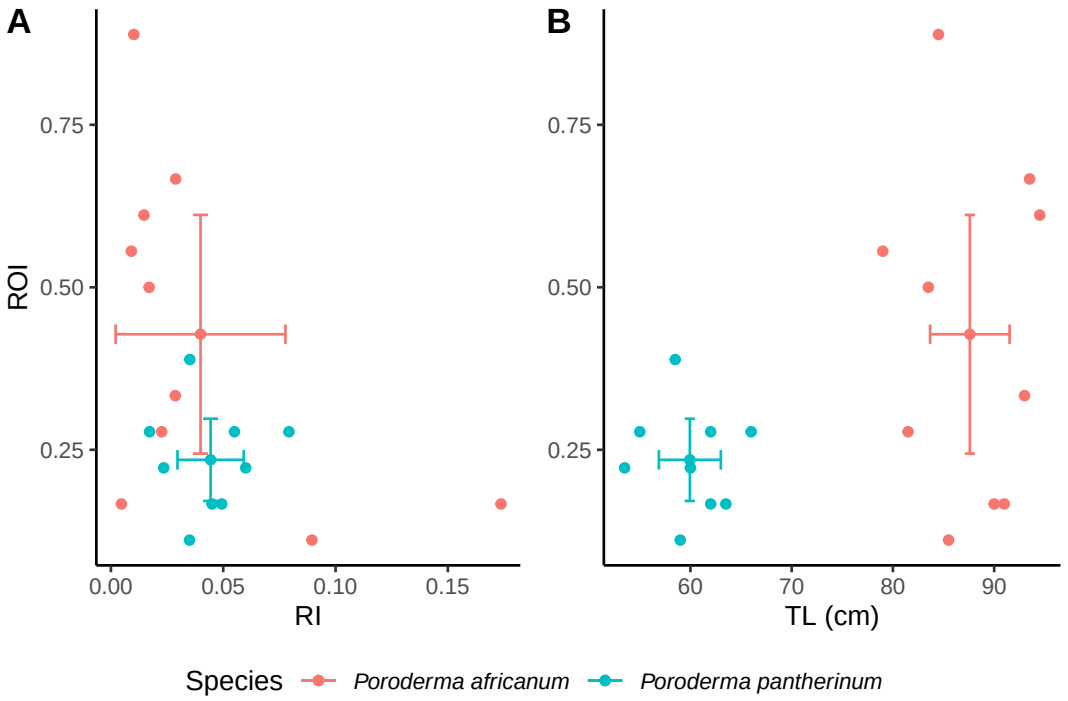


Figure 5.7: Roaming Index against (A) Residency Indices, and (B) TL (cm) for tagged *Poroderma* individuals across the Mossel Bay receiver array, with mean and 95% CI crosshairs. Each point is an individually tagged *Porodera* individual.

Table 5.3: MANOVA result of Roaming and Residency Indices against species.

	Df	**Pillai**	**approx F**	**num Df**	**den Df**	**Pr(>F)**
Species	1.00	0.20	2.01	2.00	16.00	0.17
Residuals	17.00					

To determine the tag attrition of the individuals, survival curves were generated based on how long the individuals were detected in Mossel Bay throughout this study (Figure 5.8). This showed that *P. africanum* had a slower survival decline than its congeneric: 75% was reached after 441 days for *P. africanum*, while *P. pantherinum* reached the 75% mark after 218 days. The 50% chance of survival was reached after 589 and 394 days for *P. africanum* and *P. pantherinum*, respectively. Towards the end of the study, approximately 40% of the individuals for both species were still present, with *P. africanum* having been present for 603 days and *P. pantherinum* for 393 days.

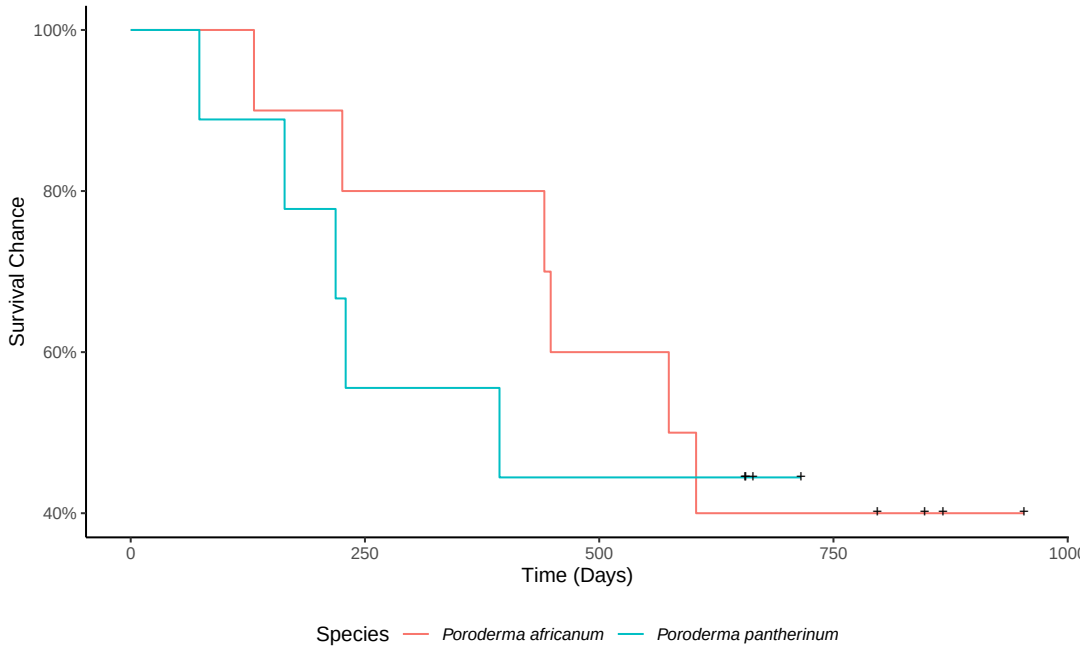


Figure 5.8: Transmitter attrition curves of acoustically tagged *P. africanum* and *P. pantherinum* in Mossel Bay over the duration of the study.

5.3.2.2 Fine-scale Rhythmic Patterns

During the study period *P. pantherinum* were on average detected almost twice as frequently as *P. africanum* (W = 29290, p < 0.001). Based on hourly detections, both species showed a similar mean proportion of detections (Figure 5.9, black; W = 25619, p = 0.215). *Poroderma pantherinum* had a significantly higher number of detections between 20:00 and 06:00, while *P. africanum* had a more uniform distribution of hourly detections.

A PERMANOVA revealed that the proportions of hourly detections were significantly different between species, sexes and sizes (Table 5.4). Mean hourly detections were significantly different from an even distribution for both *P. africanum* and *P. pantherinum* individuals (χ^2: p < 0.01). Visual examination of the individual lines showed individual variation in the hourly detections for both species.

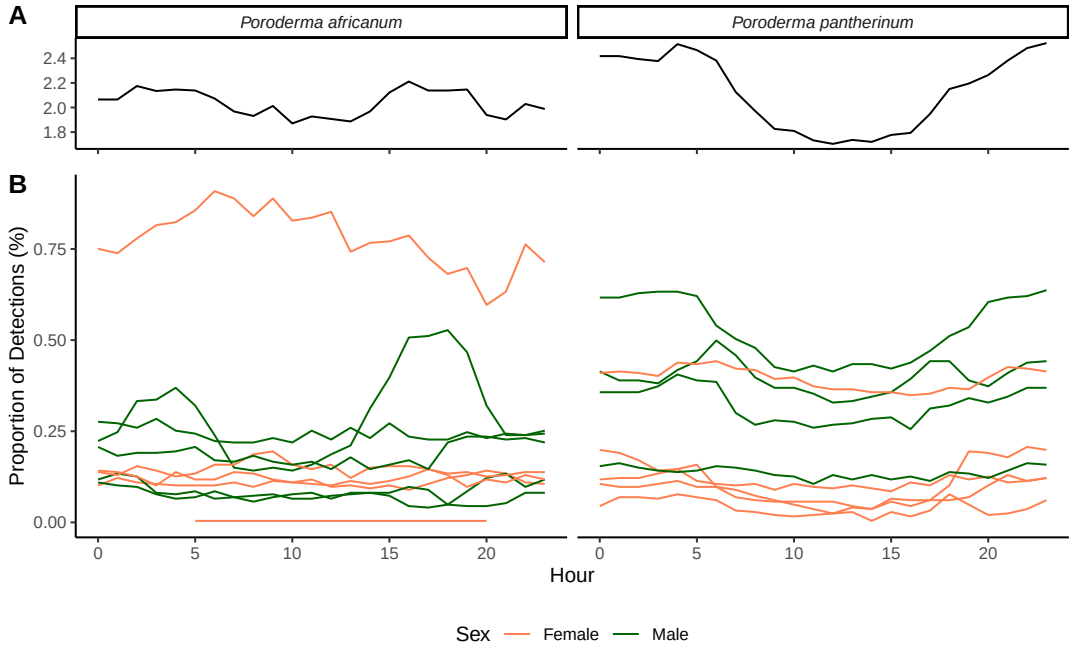


Figure 5.9: Proportion of detections of *P. africanum* and *P. pantherinum* over 24 hours. Lines were coloured for (A) the sum of the species, and (B) individually, coloured by sex.

Spectral analysis using an Fast-Fourier Transform was performed on the two species as a whole (Figure 5.10), and on nineteen individuals, ten *P. africanum* and nine *P. pantherinum* (Appendix C). The results showed that *P. africanum* had marked peaks at 12 and 24 hours, possibly indicating a strong tidal and diel rhythm. Fifty percent of the examined *P. africanum* individuals showed the diel rhythm, while 30% showed the tidal pattern. *Poroderma pantherinum*, on the other hand, showed only a general peak at 24 hours, indicating a diel rhythm.

The circular analysis was performed on the starting times (in 10-minute bins over 24 hours) for all departures from an acoustic receiver (Figure 5.11). This showed that *P. africanum* moved from one receiver to another primarily during the night (59.6%), with a strong peak (17.4%) occurring early in the night (n = 1462). The excursions were not uniformly distributed over time but significantly clustered (Rao Spacing Test, $U = 292.5$, $p < 0.05$). The time of departure for *P. pantherinum* showed a sharper contrast compared with *P. africanum*, as it was more sharply clustered

Table 5.4: Results of the PERMANOVA performed on the proportion of detections in each hour, over a 24-hour cycle, for each *Poroderma*. Independent variables included species, size (Total length in cm) and sex.

	Df	**SumsOfSqs**	**MeanSqs**	**F.Model**	**R2**	**Pr(>F)**
Species	1	0.74	0.74	6.91	0.01	0.0040
Size	1	1.04	1.04	9.66	0.02	0.0010
Sex	1	3.57	3.57	33.31	0.07	0.0010
Residuals	434	46.55	0.11		0.90	
Total	437	51.90			1.00	

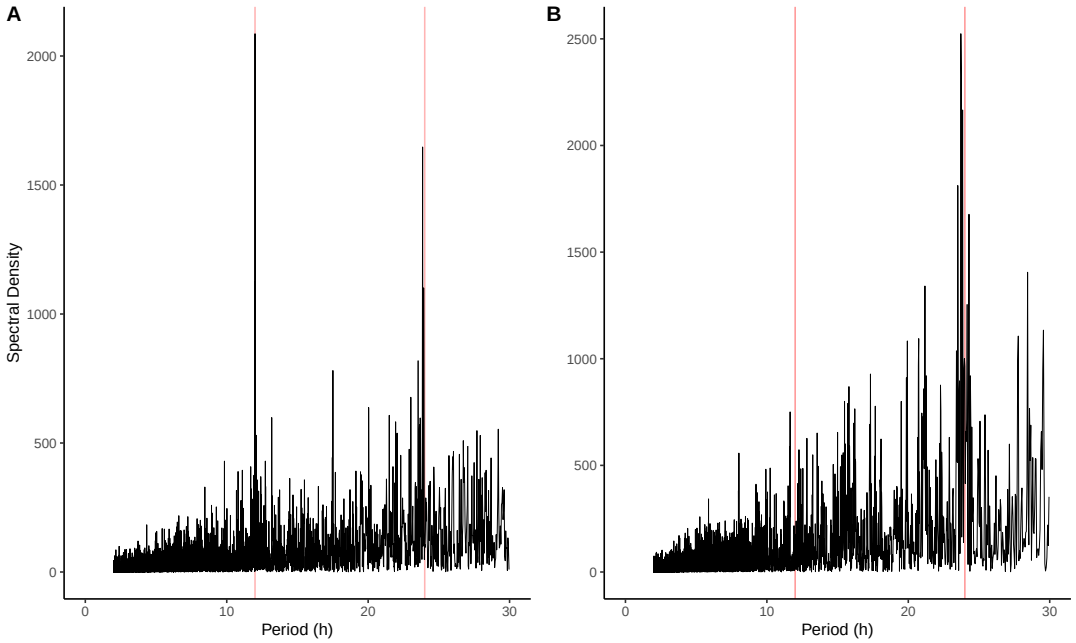


Figure 5.10: Fast-Fourier Transform showing the diel periodicity of (A) *P. africanum* and (B) *P. pantherinum* in Mossel Bay, South Africa. Red lines mark the 12 and 24 hour periods.

towards the night (76.1%: Rao Spacing Test, U = 332.69, p < 0.05), with the biggest peak (20.7%) between 01:00 and 03:00 (n = 377).

There was a significant difference in the frequency of departure from acoustic receivers between the two species (W = 5772.5, p < 0.05). While *P. africanum* showed no significant difference in departure times between the sexes (W = 1680, p = 0.125), there was a significant difference in departure times between the sexes within *P. pantherinum* (W = 983, p < 0.01). While several individuals of *P. africanum* showed increased frequencies during the austral summer months, there

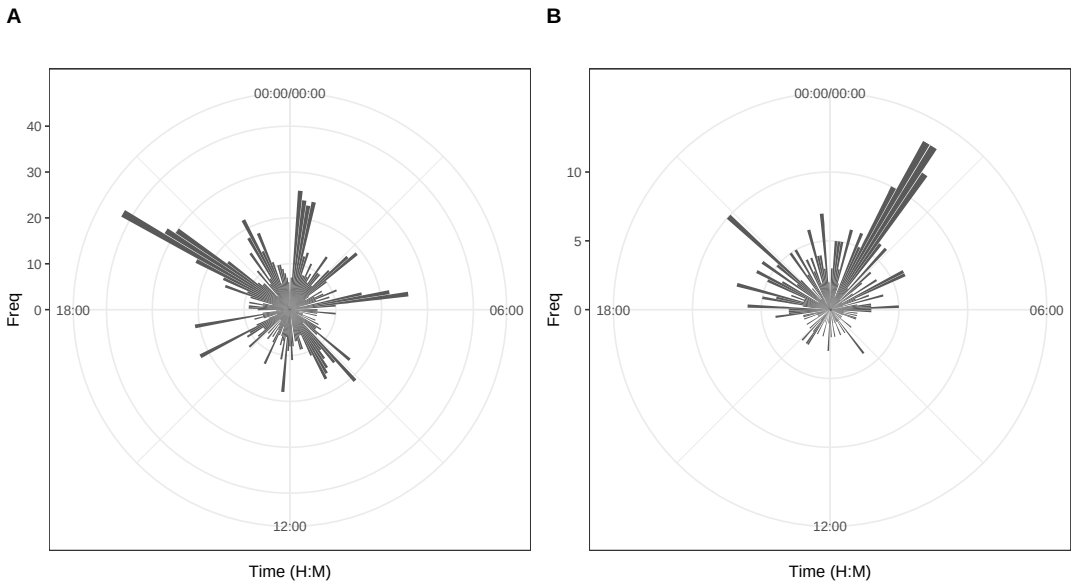


Figure 5.11: Circular plot of departure times from acoustic receivers for (A) *P. africanum* and (B) *P. pantherinum*.

was no significant differences in departure frequencies between the months for both *P. africanum* ($\chi^2 = 15.97$, p = 0.142) and *P. pantherinum* ($\chi^2 = 11.04$, p = 0.44; Figure 5.12).

5.3.2.3 Spatial Connectivity and Depth Use

During the study, *P. africanum* was detected on all 18 receivers (Figure 5.13A), while *P. pantherinum* was detected on 14 receivers in the Mossel Bay array (Figure 5.13B). *Poroderma pantherinum* were not detected on receivers that were deployed deeper than 40 m.

The monthly distance traveled between the receivers within the network revealed that *P. africanum* traveled further distances and with a higher degree of individual variation compared to *P. pantherinum* (20.97 km, 95% CI: 12.73–29.22 km; 8.56 km, 95% CI: 4.85–12.27 km, respectively; t = 2.74, p < 0.01). While several *P. africanum* individuals traveled longer distances during the austral summer between November and February, this was not consistent across the

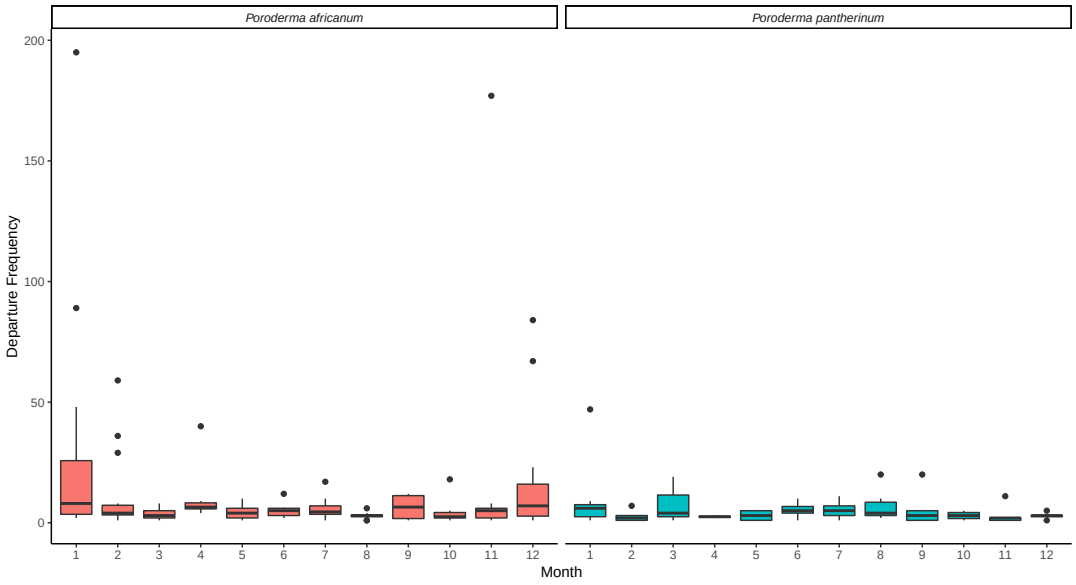


Figure 5.12: Frequency of departure from acoustic receivers for *P. africanum* and *P. pantherinum* per individual per month.

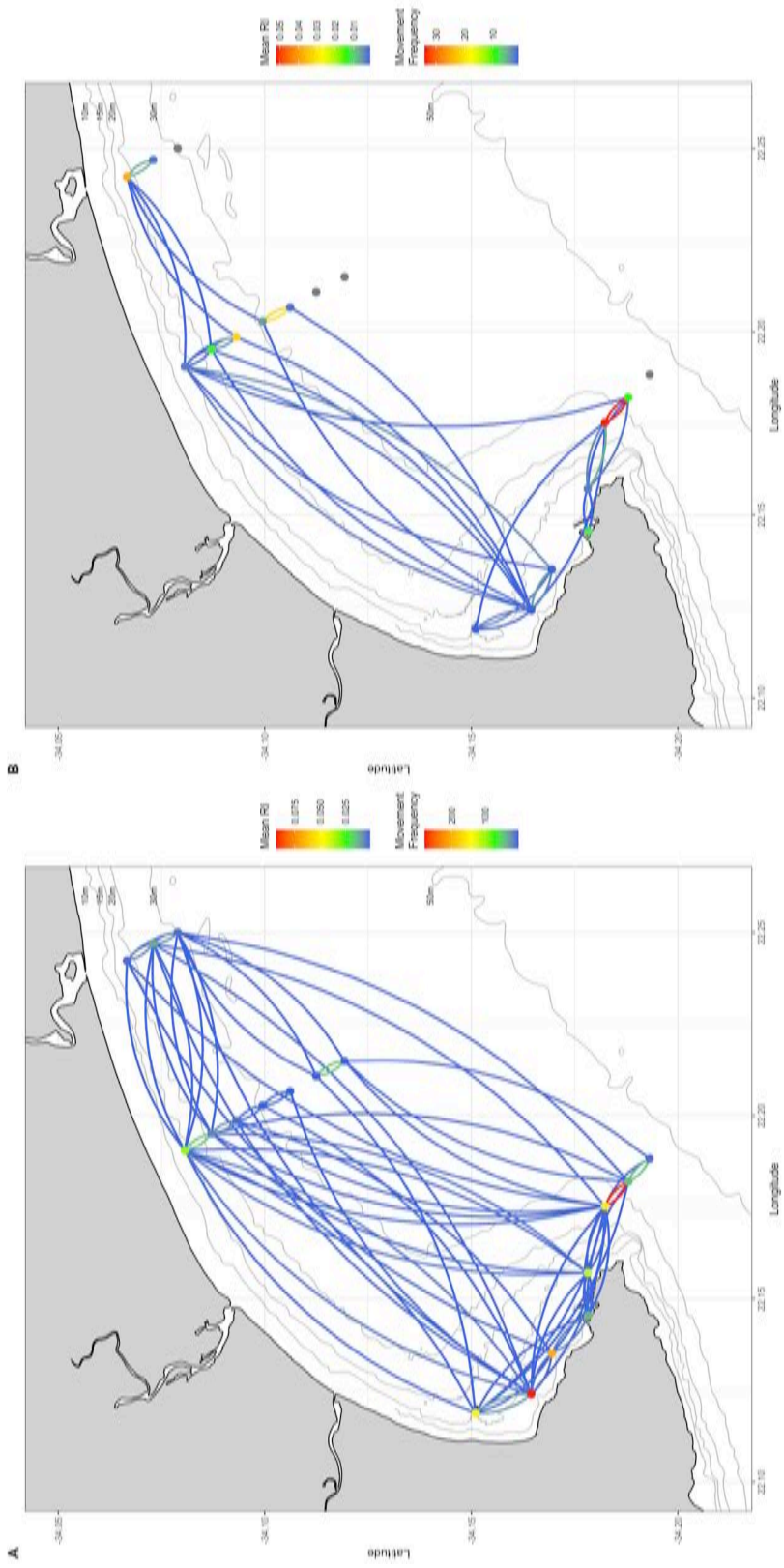


Figure 5.13: Movement network graph of (A) *P. africanum* and (B) *P. pantherinum* across the Mossel Bay receiver array from August 2015 to March 2018. Vertices are the acoustic receivers, and coloured according to the average RI, with grey indicating no detections on those receivers. Edges are movement detected between two receivers, coloured according to the frequency of those movements being detected. Created with R v3.6.2.

species, and as a result not significant. The travel distances for *P. pantherinum* remained relatively stable throughout the year (Figure 5.14), with only one individual travelling more than 50 km during one month.

While *P. africanum* showed repeated movement between neighbouring receivers such as the Seal Island and Roman's Reef (movement frequencies of 25 and 28) and between MB001 and MB002 (movement frequencies of 45 and 49), the highest movement frequency was between CSB001 and CSB002 (movement frequencies of 280 and 273). *Poroderma africanum* was the most resident on receivers in the Bay area of the network, where they were tagged, followed by the receivers at the Point. RI at individual receivers ranged from 0.001 to 0.387, with Roman's Reef having the highest average RI value with 0.093, followed by Mitch Reef (RI = 0.067) and CSB001 (RI = 0.052). The *P. africanum* network had an Edge Density of 0.25, revealing wide-ranging movement within the network. RIs were significantly higher in shallower receivers ($F[2, 75] = 4.94$, $p < 0.05$, Figure 5.15). The Betweenness of these receivers was higher than others in the network (Table 5.5), indicating that the areas around Roman's Reef and CSB001 were important for spatial connectivity. The network had an overall Clustering Coefficient of 0.44, indicating that the receivers in the network were well connected. The Clustering Coefficient of individual receivers identified movement between receivers CSB003 (CC = 0.78), GB001 (CC = 0.757) and Seal Island (CC = 0.625) as important for spatial connectivity. CSB001 and CSB002 were the receivers with the highest Eigenvector Centrality scores (0.989 and 1, respectively).

The *P. pantherinum* network had an edge density of 0.12, indicating less movement between the receivers than *P. africanum*. The highest movement frequency of *P. pantherinum* was between CSB001 and CSB002 (movement frequency of 34 both ways), followed by MB004 and MB005 (movement frequency of 20 and 21), and GB001 and GB002 (movement frequency of 5 both ways).

Similar to *P. africanum*, RIs were significantly higher in shallower receivers for

Table 5.5: Receiver metrices of *P. africanum*'s movement network.

Receiver	**Betweenness**	**Clustering Coefficient**	**Eigenvector Centrality**
Seal Island MB	14.80	0.62	0.00
Roman's Reef MB	28.72	0.32	0.00
Mitch Reef MB	9.48	0.37	0.00
Darwin Reef MB	3.10	0.52	0.01
Harbour MB	0.89	0.33	0.01
MB001	5.06	0.46	0.00
MB002	6.97	0.39	0.00
MB003	2.17	0.16	0.00
MB004	3.83	0.12	0.00
MB005	0.00	0.50	0.00
MB006	0.67	0.25	0.00
MB007	0.58	0.33	0.01
GB001	0.60	0.76	0.00
GB002	0.25	0.44	0.00
GB003	16.99	0.51	0.00
CSB001	55.47	0.30	0.99
CSB002	0.89	0.55	1.00
CSB003	0.00	0.78	0.15

P. pantherinum ($F[2, 35] = 5.75$, $p < 0.05$, Figure 5.16). The highest average RI value was at CSB001 (RI = 0.059). There was no significant difference in RI values between the two species ($W = 1179.5$, $p = 0.135$).

Several receivers showed high values of Betweenness (MB001 = 36.5, Roman's Reef = 31.567), suggesting that these sites are important for the connectivity of *P. pantherinum* across the receiver network. This was further supported by a Clustering Coefficient of 0.41, and similarly to *P. africanum*, the movement between receivers were reasonably well connected across the network. The Clustering Coefficient of individual receivers identified the areas wherein receivers MB003 (CC = 0.962), Seal Island (CC = 0.833) and Mitch Reef (CC = 0.673) were located as important for spatial connectivity. Similarly to the Eigenvector Centrality scores of the *P. africanum* network, CSB001 and CSB002 were the receivers with the highest Eigenvector Centrality scores (1 and 0.994, respectively).

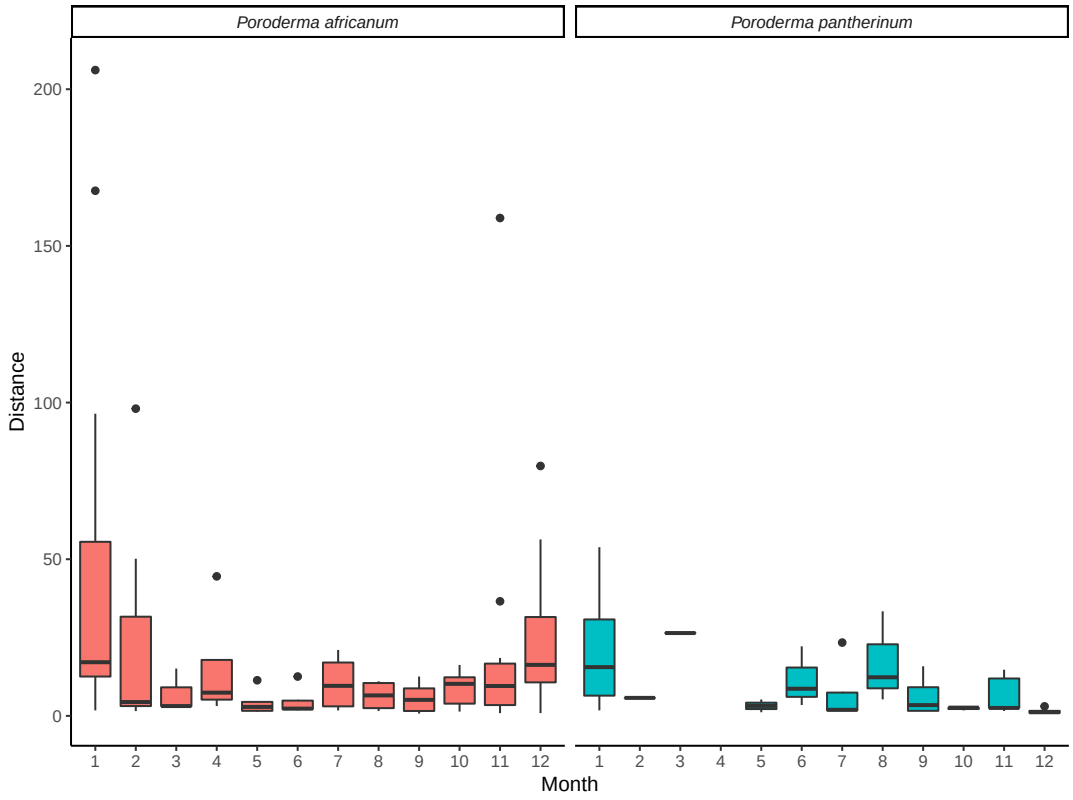


Figure 5.14: Boxplot of distance travelled by individual *Poroderma* spp. per month. The travel distance for each individual was calculated by year and month.

Table 5.6: Receiver metrices of *P. pantherinum*'s movement network.

Receiver	**Betweenness**	**Clustering Coefficient**	**Eigenvector Centrality**
Seal Island MB	0.50	0.83	0.01
Roman's Reef MB	31.57	0.29	0.02
Mitch Reef MB	0.00	0.67	0.00
Darwin Reef MB	12.00	0.29	0.16
Harbour MB	0.00	0.00	0.01
MB001	36.50	0.40	0.01
MB002	3.20	0.51	0.00
MB003	1.60	0.96	0.00
MB004	1.60	0.25	0.00
MB005	0.00	0.38	0.00
MB006	0.00		0.00
MB007	0.00		0.00
GB001	15.53	0.14	0.00
GB002	0.00	0.00	0.00
GB003	0.00		0.00
CSB001	1.00	0.41	1.00
CSB002	19.00	0.50	0.99
CSB003	0.00		0.00

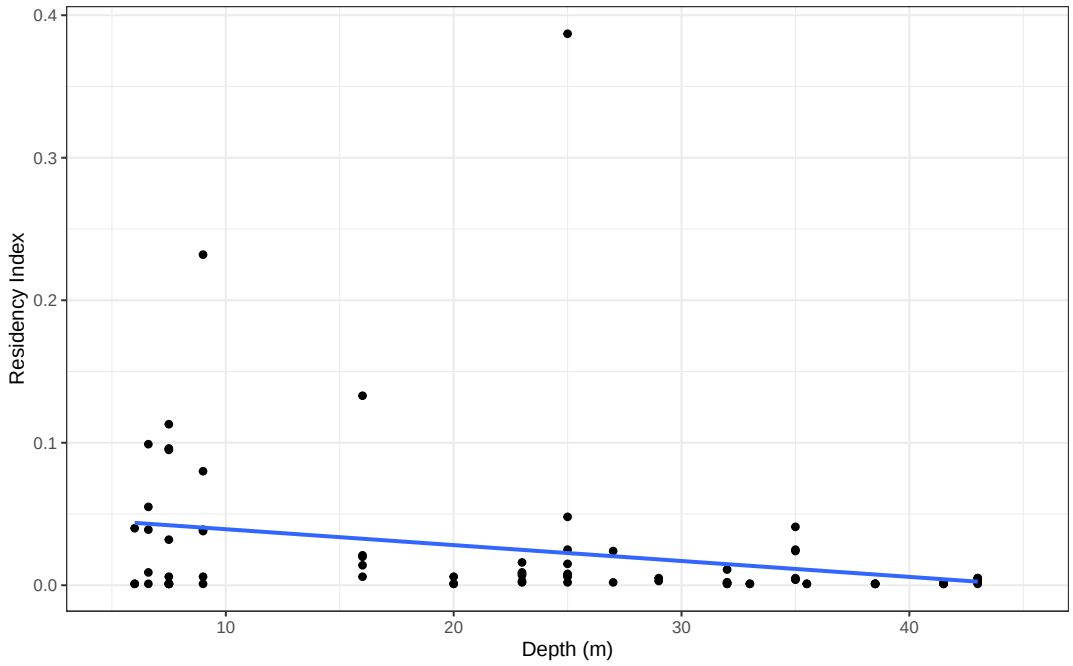


Figure 5.15: Scatterplot of Residency Indices against depth for *P. africanum* with fitted `lm`-smooth line.

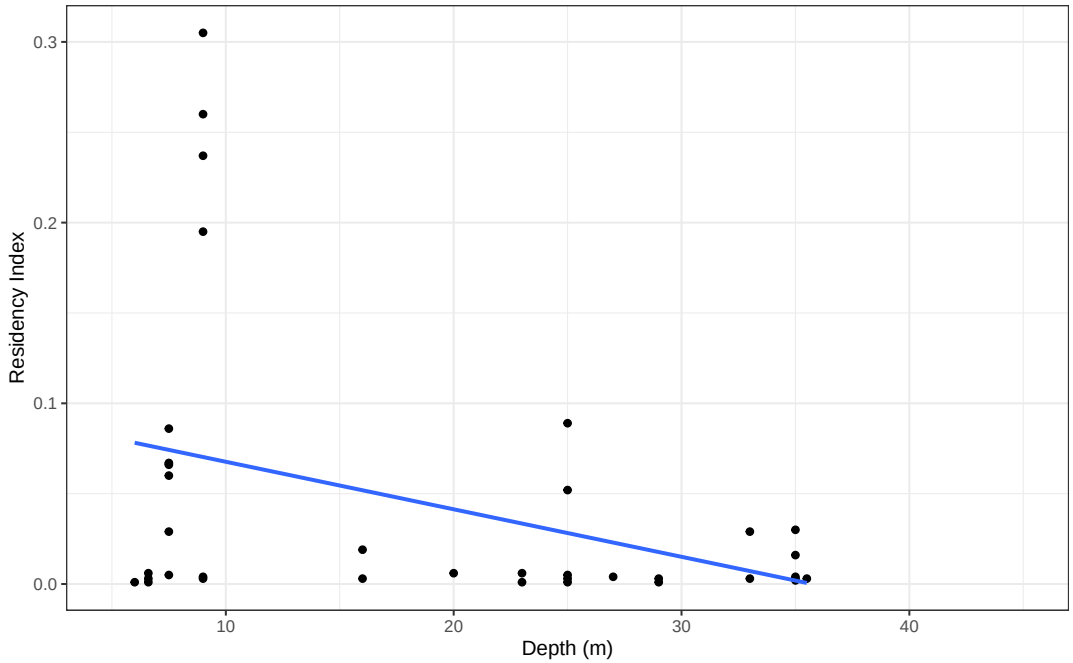


Figure 5.16: Scatterplot of Residency Indices against Depth for *P. pantherinum* with fitted `lm`-smooth line.

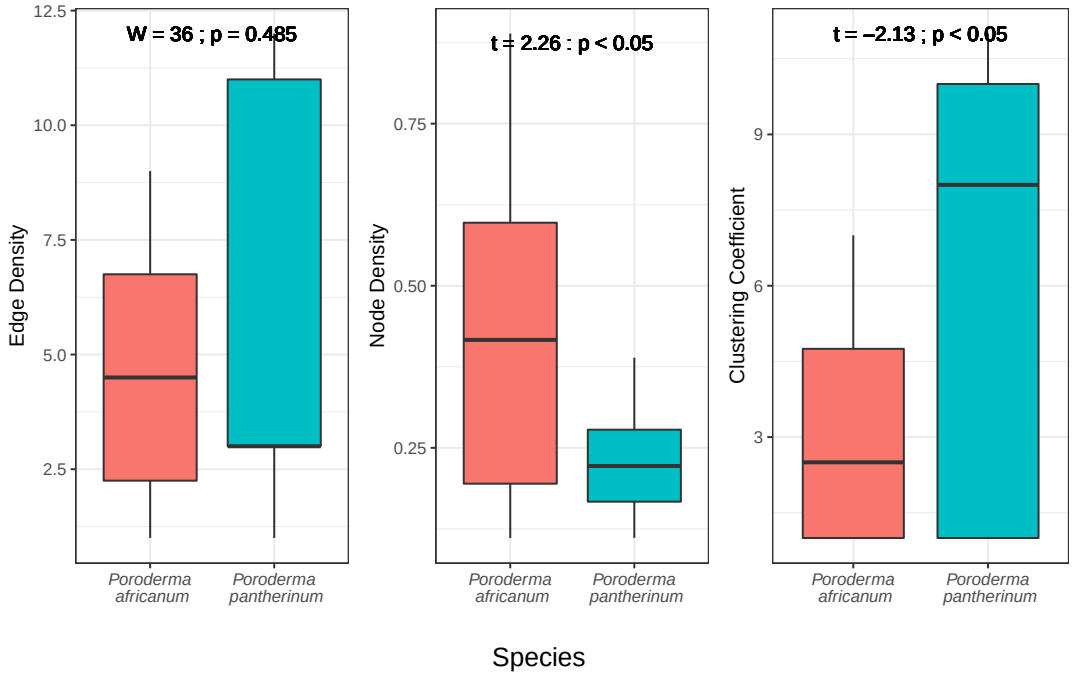


Figure 5.17: Boxplots of network metrices for individual *P. africanum* and *P. pantherinum*, with p-values for associated t- and wilcox-sum rank tests.

5.4 Discussion

Results from both mark-recapture and passive acoustic telemetry indicated that both *Poroderma* spp. were highly resident, with limited lateral movement. Closer examination of the movement behaviour using acoustic telemetry showed small niche differentiation between the two species along spatial and temporal axes, with a large degree of individual variation within both species. Both *Poroderma* spp. were detected across the full extend of the acoustic receiver array, while individuals within each species utilized the array differently. *Poroderma pantherinum* was more resident, while *P. africanum* showed broader movement.

5.4.1 Mark-Recapture

Both species exhibited high site fidelity, with >70% of the tagged individuals being recaptured at the site of first capture (tagging location). The movement behaviour for both species was consistent throughout their ranges. This could be attributed to the notion that the majority of scyliorhinidae are generally weak swimmers over great distances (Ebert and Dando, 2020). The recapture rate was high (±10%) as the majority of elasmobranch mark-recapture studies have a recapture rate less than 5% (Kohler and Turner, 2001), and only 43 out of 374 species in national ORI-CFTP had a recapture rate above 10% (ORI: `https://www.oritag.org.za/Leaderboard`; accessed December 2020). The results showed no major differences in the movement behaviour between the two species.

The mark-recapture data also revealed that the high site fidelity was consistent throughout the distribution both species. Several of the individuals with a high time of liberty were recaptured at the same location, showing that both species have an extremely high site fidelity. High site fidelity is seen in other chondrichthyans, such as *Heterodontus francisci* (horn shark), *Carcharhinus melanopterus* (blacktip reef shark), and *T. obesus* (Kohler and Turner, 2001), and South African teleost, such

as *Chrysoblephus laticeps* (red roman; Kerwath *et al.*, 2007) and *Dinoperca petersi* (lampfish; Mann *et al.*, 2020). Within South Africa, the commonality of high site fidelity with teleosts might suggest that conservation management protocols targeted at reef fish as a group could benefit the *Poroderma* spp. within that community.

The survivability, emigration and residency of *P. africanum* using mark-recapture in Mossel Bay were further explored in Grusd *et al.* (2019). Within that study, *P. africanum* showed an apparent survival of 0.716/year (range: 0 to 1/year), with a declining abundance between 2012 and 2016. In Grusd *et al.* (2019) the species was suggested to be highly resident, supporting the results of this study and others (Escobar-Porras, 2009). The best-fit model in Grusd *et al.* (2019) included a random constant temporary emigration constraint, indicating that the best abundance model included individuals migrating between an observable and unobservable state, either off the target reefs or into hiding places.

Examination of the broadscale movement behaviour of the two species through ORI-CFTP data is advantageous, as the dataset contains very long-term data, even exceeding the current known lifespan of both species, and covers the full distribution of both species. However, the records of *P. pantherinum* individuals in Namibia reveals an underlying problem of possible misidentification of tagged species. Additionally, this method provides low-resolution information on movement behaviour, as capture and recapture localities are based on a 1 km resolution (Dunlop *et al.*, 2013), and dependent on the recapture of the individual. This is inconvenient for behavioural studies for the *Poroderma* spp., as they are highly resident and it does not provide any insight on their behaviour on a smaller scale. Therefore passive acoustic telemetry was used to examine the small-scale movement behaviour.

5.4.2 Passive Acoustic Telemetry

The acoustic telemetry study conducted on 11 *P. africanum* and 10 *P. pantherinum* individuals in Mossel Bay indicated that on a small scale (<15 km) there were significant differences in the behaviour of the two *Poroderma* species. While the sample size was relatively small, it was representative to the relative abundance of the species (especially *P. pantherinum*) in the area (Chapter 3). This was on-par with similar studies involving acoustic telemetry performed elsewhere around the South African coast (Johnson *et al.*, 2009; Kerwath *et al.*, 2009). *Poroderma pantherinum* was detected twice as frequently as *P. africanum*, while the latter showed a higher degree of movement through the receiver array. The mark-recapture results revealed that both species could move further than the full extent of the receiver network in Mossel Bay.

Passive acoustic telemetry was considered the most effective method to gain an initial understanding of where and when individuals of the *Poroderma* spp. moved. While passive acoustic telemetry was used to study *Poroderma* spp. in the Tsitsikamma Marine Protected Area, this was limited to presence/absence using two VR2 receivers in two local embayments (each ±100 m wide; Escobar-Porras, 2009).

There was a significant difference in residency using CRT between the two species, with *P. pantherinum* showing on average a higher residency within covered areas of the bay compared to *P. africanum*. In addition to the increased movement behaviour of *P. africanum*, with a higher average roaming index, this suggests that this species departs reefs more frequently than its congeneric, and covers a wider area of the receiver array. While this could suggest a degree of avoidance between the two species, they were detected on the same receivers relatively frequently on the reefs where the individuals were tagged. However, while the average roaming

index for *P. africanum* was higher than *P. pantherinum*, the variation in roaming index for this species was also higher, with half of the tagged *P. africanum* individuals having a similar roaming index to *P. pantherinum*. This was not linked to differences in size of the tagged individuals, suggesting either an individual preference for the varying movement behaviours within the species, or due to a gap in receiver coverage of where the individuals travel to (e.g. offshore). The non-significant differences in departure frequency from the receivers throughout the year for both species suggests that the rate of departure from the detection range of acoustic receivers remained consistent throughout the year.

Poroderma pantherinum showed a higher proportion of hourly detections during the night, while *P. africanum* was more homogenously detected throughout the day. This is seen in other elasmobranchs as well, with different species being active during different times of day (Speed *et al.*, 2011). The underlying patterns in acoustic detections of the *Poroderma* spp. revealed a very complicated interplay between diel and tidal rhythms. There was a strong diel periodicity in both *Poroderma* spp., such as seen in other elasmobranchs (Filmalter, 2015; Elston, 2018), while *P. africanum* showed a strong tidal cycle as well. The difference in environmental influences could be explained by differences in diet and hunting behaviour (see Chapter 4 and Chapter 6). As both *Poroderma* spp. showed a primarily nocturnal transiting behaviour between receivers, this would likely indicate a nocturnal hunting behaviour for both species. Future studies looking at the diel detection patterns of the species should include measures to account for variability in detection range as a result of reef structure (Welsh *et al.*, 2012), background noise (Kessel *et al.*, 2014), and diel detection variation (Payne *et al.*, 2010).

While the tidal rhythm could be explained by the shallowness of the reef, resulting in the exclusion of detections due to masking caused by wave action and strong tidal currents, there could be other underlying forces at play. Tidal rhythms are drivers of

movement in other elasmobranch species, though often associated with planktonic organisms (Shepard *et al.*, 2006). Further studies on activity and migration would clarify rhythmic patterns related to diel and tidal forces (Kelly *et al.*, 2019).

The departure times of *P. africanum* showed several smaller clusters between 19:00 and 05:00, while the departure times for *P. pantherinum* was primarily grouped between 01:00 and 03:00. Movements were recorded if there were consecutive detections on the subsequent receiver, or if individuals were not detected on a receiver for more than 24 h, assuming they had left the detection range of the receiver. Exclusion of the movement between the receivers with the highest movement frequency (CSB001 and CSB002) still showed this clustering of departure times. As these two receivers were located near the same reef of Cape St. Blaize, the clustering of departure times was indicative of animals leaving their home-reef, rather than patrolling the reef. The results suggest temporal segregation during nocturnal activity, with the movement of *P. africanum* primarily limited to early- and late-night periods, and *P. pantherinum* clustered around the middle of the night.

The movement of species at night could be a survival strategy to avoid predation (Hammerschlag *et al.*, 2017). To confirm this for the *Poroderma* spp., all major predators of these two species would need to be identified, and their diurnal activity patterns explored. *Notorhynchus cepedianus* and *Arctocephalus pusillus pusillus* are known to occur in the Mossel Bay area (Engelbrecht *et al.*, 2019; Morse *et al.*, 2019) and are known predators of the *Poroderma* spp. (Ebert, 1991; Barnett *et al.*, 2010a; Martin, 2004). While they are both known to be nocturnally active, their activity patterns at night would need to be explored to determine whether their nocturnal activity is related to predations on the *Poroderma* spp. The nocturnal activity of these predators is unlikely to influence the nocturnal departure times of the *Poroderma* spp. as a result of predator avoidance, as predators such as *N. cepedianus* and *A. pusillus pusillus* are more mobile than the benthic Scyliorhinidae,

and would be able to traverse from one reef to another as well. Nevertheless, the possibility should not be excluded. The use of accelerometer transmitters would confirm and elucidate such activity patterns of *Poroderma* spp. in the future.

Conversely, the nocturnal activity of the *Poroderma* spp. could link to the activity patterns of their prey as well, as a prey item of *P. pantherinum*, *Loligo vulgaris reynaudii* (Cape Hope squid; Chapter 4), is known to be nocturnally active (Downey *et al.*, 2010). Further examination of the activity pattern of the various prey species of both *Poroderma* spp. would elucidate whether the diel activity of the study species would be an adaptive response to hunt when their prey is most active.

Five receivers were strategically placed along the western side of Mossel Bay, supplementing the already exisitng ATAP acoustic receiver network, providing an understanding of the coastal movement behaviour of the two *Poroderma* spp. The low residency suggested that both species departed the reef frequently, while maintaining a high site fidelity. Individuals of both species travelled across the array of receivers, the far sides of which were covered by sandstone reefs. *Poroderma pantherinum* individuals spend significant time in the areas of the MB and GB receiver curtains. The movement across the bay also indicated that individuals of both species cross the Mossel Bay area, traversing from one reef system to another. During these crossings, *P. pantherinum* remained close inshore shore, being detected on receivers often in waters less than 30 metres depth.

While *P. pantherinum* showed low intra-specific variation in roaming behaviour, there was a large amount of intra-specific variation in roaming behaviour in *P. africanum*, with some individuals being detected on the majority of receivers (i.e., 16 out of 18 receivers), while others on only a fraction (i.e., 2 out of 18 receivers). There was no correlation between the size of the individual and the ROI for either species, indicating that the roaming behaviour was uniform for the sizes tagged. However,

as *P. africanum* are generally bigger than *P. pantherinum*, larger size might have influence on a greater tendancy to roam. This might also suggest that by having a fraction of the *P. africanum* population travel wider, this lessens competition with a higher resident species. This has been seen between other species of reef sharks, whereby variation in space use avoids compeititon due to similarity in diet (Heupel *et al.*, 2018b).

The area off Cape St. Blaize was shown to be an area of high importance for both *Poroderma* spp., exhibiting the highest number of transitions between receivers and Eigenvector Centrality scores for both species. A sandstone reef, Bob's Bank, is located near the point (Cawthra *et al.*, 2016). As all *Poroderma* individuals were tagged along the western edge of the bay, this suggests that there is a high degree of site fidelity for both species. The high transitions between receivers can be explained by the two receivers being located on the top of the reef, suggesting that the movement is due to individuals patrolling across the reef. The inshore bay area and Groot Brak receiver curtain (GB001–3) were suggested to be of high importance for the connectivity of the *P. africanum* population, while the Klein Brak receiver curtain (MB001–7) was shown to be very important for the connectivity of the *P. pantherinum* population

This study focused on the movement behaviour of *Poroderma* spp. across Mossel Bay as a whole, with strategically placed receivers at smaller reefs along the western edge of the bay. This study showed that individuals of the *Poroderma* spp. moved further than to neighbouring reefs, and could travel laterally well over 15 km. One such reef system that was not covered by the acoustic array was Hartenbos Reef, located between Seal Island and Klein Brak. The importance of this reef as a transition area is showcased by the number of transitions that occur between the Roman's Reef and Seal Island receivers, and the Klein Brak receiver curtain. Periods of absences of *Poroderma* individuals from the Roman's Reef and Seal Island receivers can additionally suggest foraging surveys onto Hartenbos

Reef, after which the individual returns to their home-reef without moving on towards the Klein Brak receiver curtain. Expanding the receiver network to cover any departure directions from the target receiver would account for periods of absences at the target reefs. This way fine-scale movement over a larger area would provide a higher resolution on the degree of connectivity between important reef sites. However, this was not the aim of this study and would require doubling or tripling the number of receivers used to accomplish this.

The nearest receivers outside the Mossel Bay network were a single receiver in Kanon, an estuarine receiver in Knysna, with the next receiver array in Plettenberg Bay (Cowley *et al.*, 2017). While some individuals were shown to travel this far through mark-recapture, further exploration would be needed to determine whether establishing a network array in these areas is enough to capture the movement between neighbouring populations. Genetic analysis would provide additional information on the population structure and whether enough gene flow occurs between local populations that are under threat to ensure the survival of populations without resulting in a genetic bottleneck (Bester-van der Merwe and Gledhill, 2015).

This novel understanding of the movement behaviour of these species can act as a foundation for future research, and a basis of which adjustments can be made to gain further clarification on the species' behaviour. To get a higher resolution of the foraging behaviour of the species', future research would benefit from the setup of a high-density receiver network, whereby the receiver covering the reef is surrounded by several other receivers. This would confirm whether the absence of individuals at receivers covering the reefs means a true absence or failure to detect them. The setup of a fine-scale positioning system (e.g., Innovasea VPS) would provide a high-resolution understanding of their movement behaviour, and get a better idea of the home ranges of tagged individuals. This would allow for the

obtainment of movement metrices useful in identifying movement syndromes (Abrahms *et al.*, 2017). Additionally, active tracking of tagged individuals would result in similar metrices, however, this requires more field hours due to the uncertainty of when the target animal leaves their home-reef.

Long residency periods within areas of the bay, and higher residency times on receivers associated with sandstone reefs, suggests that reefs are of high importance to the *Poroderma* spp. This is corroborated in other research as well (de Vos *et al.*, 2015). However, further expansion of the receiver network across other habitats would further corroborate habitat preference of the species. Globally reefs have degraded significantly, with climate change and local human impacts, such as fishing, suggested as causes for these events (Mora *et al.*, 2011). The dependence of *Poroderma* spp. on reef systems makes them particularly vulnerable to climate change and human impacts, and management and conservation efforts on these species should focus on the protection of these habitats.

The inshore movement makes Scyliorhinidae susceptible to threats from various sources of fishing (Field *et al.*, 2009), such as gillnet fisheries (Hutchings and Lamberth, 2002), inshore trawl fishery (Attwood *et al.*, 2011) and recreational shore-anglers (Ebert and Stehmann, 2013). While movement speed would examine whether the species are more susceptible to one type of fisheries or another (Lennox *et al.*, 2017), due to the resolution of the acoustic receivers and fine-scale movement behaviour of the *Poroderma* spp., gaining accurate and representable movement speeds across the area was not possible within the scope of this study. However, further examination using accelerometers to determine activity patterns in different areas of the bay could examine how susceptible the species are to fishing pressures while moving throughout their home range (Lennox *et al.*, 2017).

Both species showed a high degree of individual variation in their movement behaviour, which makes management and conservation considerations for both species difficult (Speed *et al.*, 2010). The design of marine protected areas around

smaller elasmobranchs in Southern Africa should identify sites of high concentrations and importance, cover entire reef-systems, and include an area large enough to accommodate the home range of populations. While the design of the receiver network did not allow for the calculations of Kernel Density Estimates, as individuals of both species were seen traversing the entirety of the acoustic receiver network in Mossel Bay, a minimum diameter of 10 km should be considered for the design of MPAs for the protection of these benthic chondrichthyans (see Chapter 6).

Research on catshark movement using passive acoustic telemetry has been sparse in the past, with some research in Australia (Awruch *et al.*, 2012), the UK (Jacoby *et al.*, 2012) and Ireland (Sims *et al.*, 2005). These studies have also seen individual variation in movement behaviour (Jacoby *et al.*, 2012), and a high degree of site fidelity (Awruch *et al.*, 2012). While this is nowhere near conclusive of a generalized statement of Scyliorhinidae behaviour, the results garnered in this chapter add to a similar narrative on Scyliorhinidae regardless of species or locality.

Chapter 6

General Discussion

The purpose of this study was to examine how *Poroderma africanum* and *P. pantherinum* co-exist within the Mossel Bay area through adopting a multidisciplinary approach. The information obtained provides a better understanding of the ecology of these two sympatric species in Mossel Bay, and relevant information for future management and/or conservation initiatives. This study revealed that the two *Poroderma* spp. showed distinct differences in their ecology, with a lot of intraspecific variation, making management considerations for their conservation complicated.

6.1 Sympatry of the *Poroderma* spp. Along Ecological Axes

Multiple theories exist regarding patterns of co-existence in sympatric species, amongst them the theory of niche differentiation and the hypothesis of neutrality (Vellend, 2016). The theory of niche differentiation suggests that species partition resources along one or more ecological axes, such as time, food, and/or space. This ensures lower inter-specific competition, allowing for coexistence (Schoener, 1974). The hypothesis of neutrality on the other hand suggests that co-occurring species do not need to differentiate in resource use if their competitive abilities are equal,

thus removing the effect of competitive exclusion (Hubbell, 2005).

There is the consensus that both niche and neutral hypotheses explain patterns of species co-occurrence present in nature (Stokes and Archer, 2010). Theoretical models highlight that species can co-exist, if they are sufficiently similar or sufficiently dissimilar from each other, under the condition that food is not a limiting factor (Scheffer and van Nes, 2006; Vellend, 2016).

As the two *Poroderma* spp. are morphologically very similar, with their primary differences being colour pattern and size (maximum ∼100 cm TL vs 84 cm TL for *P. africanum* and *P. pantherinum*, respectively), the question is whether their ecologies are similar enough to fall under Hubbell (2005)'s hypothesis of neutrality, or Schoener (1974)'s theory of niche differentiation.

As spatio-temporal patterns of species abundance influence the strength of trophic interactions between and amongst different layers of the trophic web, the movement of both predators and prey helps determine those patterns of abundance (Andrews and Harvey, 2013). Through the use of three different techniques, the three ecological axes of time, food and space are explored with a focus on the *Poroderma* spp. The differences along each ecological axis will be discussed in the following sections, by integrating the results obtained from the relevant techniques.

6.1.1 *Poroderma* spp. Along the Temporal Ecological Axis

Species occupying a similar niche in the same habitat can be separated along a temporal scale to avoid competition (Kronfeld-Schor and Dayan, 2003). This has been reported in species such as dung beetles (Caveney *et al.*, 1995), big cats (Palomares and Caro, 1999; Schaller, 2009; Romero-Muñoz *et al.*, 2010), and freshwater fish larvae (Shuai *et al.*, 2016).

This study revealed several instances of separation along a temporal ecological axis between the two *Poroderma* spp. *Poroderma africanum* departed the receivers more frequently than *P. pantherinum* (1462 for *P. africanum* against 377 for *P.*

pantherinum), suggesting that *P. africanum* depart the area the receivers cover more frequently than their congenerics. Additionally, the departure times from receivers showed a temporal difference between the two species, with *P. pantherinum* showing a peak in departure times in the middle of the night, while *P. africanum* showed several peaks in the early evening and throughout the night. This has been seen in other species around the world, such as in Australia with *Carcharhinus melanopterus* (blacktip reef shark) and *Carcharhinus amblyrhynchos* (grey reef shark) being primarily detected around midday, while juvenile *C. melanopterus* and *Negaprion acutidens* (sicklefin lemon sharks) being primarily detected in the morning, respectively (Speed *et al.*, 2011); and in the Carribean where *Carcharhinus acronotus* (blacknose sharks) were primarily nocturnal, while *Mustelus canis* (smooth dogfish) and *Squalus acanthias* (spiny dogfish) were primarily found during the mid-afternoon (Bangley and Rulifson, 2017).

Diel activity could be caused as a reaction along the trophic foodweb, with predator avoidance (Hammerschlag *et al.*, 2017) or prey activity (Cunningham *et al.*, 2019) causing the nocturnal activity of the *Poroderma* spp. This would require further examination of the diurnal activity of the predators of the *Poroderma* spp. Conversely, the nocturnal activity of *P. pantherinum* could be correlated to the prey activity, such as the nocturnally active cephalopods (Downey *et al.*, 2010), which was the second most important prey species in the species' diet (Chapter 4). Both species showed diel rhythms in detections, with *P. africanum* showing a tidal rhythm as well.

Baited remote underwater video systems (BRUVs) were used to examine the relative abundance of the two *Poroderma* spp. over a multi-year period and explore the temporal differences along seasonal variation. This revealed that *P. africanum* had greater seasonal variability based on the Relative Abundance, which was higher during winter compared to summer, while *P. pantherinum* abundance varied little over seasons. Additionally, the Relative Abundance of both species was influenced

by Sea Surface Temperature and lunar coverage, with *P. africanum* showing a strong correlation with tidal height as well.

Seasonal variation in abundance has been shown to underpin species coexistence by minimizing competition (Shimadzu *et al.*, 2013). Seasonal variation in abundance is common in many elasmobranch species (Vaudo and Heithaus, 2009; Barnett and Semmens, 2012; Housiaux *et al.*, 2019). For example in False Bay, South Africa *Galeorhinus galeus* (soupfin shark), *Halaelurus natalensis* and *Mustelus mustelus* (smoothhound shark) showed higher Relative Abundances in the austral summer than winter (de Vos *et al.*, 2015). In this study the Relative Abundance of *P. africanum* was higher during the austral winter, similarly as seen in False Bay (de Vos *et al.*, 2015), while the overall ichthyofaunal assemblage diversity was lower during this period. Results indicate that *P. africanum* is a generalist predator, this would suggest the species avoids competition with its congeneric by providing a diffused predation pressure upon the ecosystem when the diversity is at its lowest, while avoiding predating on the primary prey of *P. pantherinum*, which is present throughout the year (Oosthuizen and Smale, 2003).

Examination of the Relative Abundance for *P. africanum* showed a declining trend throughout the study period. This pattern was corroborated by Grusd *et al.* (2019), which showed a similar declining abundance for *P. africanum* using mark-recapture data in the same area from September 2012 to July 2016. Tag attrition curves generated for the acoustically tagged individuals also revealed a decline over time. While a decline in tags detected in an area could be expected as a result of tag failure, natural mortality or migration, the rate at which this happened (50% after 1.6 years) suggested that they either emigrated from the area, or removal of individuals were removed from the ecosystem. Tag attrition of *P. pantherinum* showed a similar decline as its congeneric (50% after 1.1 years).

However, the Relative Abundance of *P. pantherinum* remained stable during the

study period, suggesting that perhaps new individuals enter the study area. This, in conjunction with the mark-recapture data, suggests that there might be small lateral movement along the shoreline for the entire species. This would require further exploration, through the use of stock assessments around the South African coast. The Relative Abundance of *P. pantherinum* was relatively low, and any population declines could be concealed by low sightings.

6.1.2 *Poroderma* spp. Along the Trophic Ecological Axis

To understand the ecological role of a species within a food web, identifying their trophic interactions and positions within the food web is critically important. Due to their intermediate trophic position, understanding the trophic ecology of mesopredators is particularly relevant (Vaudo and Heithaus, 2011; Ritchie and Johnson, 2009). Resource partitioning has been suggested as a possible mechanism for the coexistence of predators (Navia *et al.*, 2016).

While there was a partial overlap in diet between the two species, *P. pantherinum* showed a highly specialist diet towards cephalopods, while *P. africanum* showed a more generalist diet composed of fish, molluscs and crustaceans, yet highly influenced by anthropogenic sources. Both species showed an ontogenetic shift in diet correlated to reaching sexual maturity. The partial dietary niche overlap showed that while there could be some level of competition between the two species, the resource partitioning allows for co-existence. However, individual specialisation within a generalist species might complicate this co-existence, as this would inflate competition between a subpopulation of one species and the full population of another (Vander Zanden *et al.*, 2010; Araújo *et al.*, 2011). This would require further examination of stable-isotope signatures of the two species to identify whether individual specialisation within *P. africanum* is occurring.

Additionally, competition between the two species may be limited, despite

partially overlapping niches, if prey is not a limiting factor (Forero *et al.*, 2004; Dehnhard *et al.*, 2020). Further examination of the various prey densities in the area would elucidate the more fine-scale reasoning for niche differentiation between the two species.

The prey items in the stomach content of both species partially overlapped with the species found on the BRUV deployments. These included (but were not limited to) *Octopus vulgaris*, *Chirodactylus brachydactylus*, *Diplodus capensis* and *Scartella emarginata* (maned blenny). However, not all free-swimming species found in the stomach content were seen on the BRUV. Most notably an *Hippocampus capensis* and a juvenile *Callorhinchus capensis* were found in the stomach of *P. africanum*, and *Sepia* spp. in the stomach of both *Poroderma* spp.

The gastric lavage done on the *P. africanum* individual containing *C. capensis* was performed just southeast off the Cape St. Blaize peninsula. While the species is known to occur in the Mossel Bay area (pers. obs.), none of the BRUV deployments performed in this study sighted *C. capensis* on any of the reefs in Mossel Bay. Additionally *C. capensis* is known to be a sand-associated species, laying its eggs on sand substrate (Freer and Griffiths, 1993). Therefore *P. africanum* likely forayed off their reef and consumed this individual off its home reef.

Sepia spp. were consumed by both *Poroderma* spp. across various sampling locations around Mossel Bay. However, *Sepia* spp. were not seen on any of the BRUV deployments along the Mossel Bay reefs, despite their both diurnal and nocturnal activities (Downey *et al.*, 2010). Additionally, the digestion times of these stomach items suggest that the majority of the stomach content was eaten within two days before sampling. This adds to the hypothesis that *Poroderma* spp. leave their home reefs periodically to prey on species not found on the reefs, and might be the reason why *P. africanum* shows a wider movement behaviour compared to its congeneric.

Another important part of the diet of both species was *O. vulgaris*. This species

was frequently observed on the BRUV deployments, and *P. africanum* has been seen attacking *O. vulgaris* on a few occasions. While no actual predation was recorded on the BRUV, this does showcase the trophic relationship between the two species, and the possibility of antagonistic interactions between different species around the bait canister (Dunlop *et al.*, 2014).

While this study was performed in an altered ecosystem, the decline in abundance did not seem to be related to a lack of food resources. This is evident in the low number of empty stomachs and the availability (and consumption) of discarded bait by *P. africanum*. This also shows the adaptability of the species to changing food resources, and possible evidence of opportunistic feeding behaviour and habituation to human activities, such as seen with *Carcharhinus leucas* (bull shark) in Fiji (Brunnschweiler and Barnett, 2013) or *Triaenodon obesus* (white tip reef shark) in Australia (Fitzpatrick *et al.*, 2011).

While discarded bait made up a large portion of the stomach content of *P. africanum*, not all items classified as bait could be linked to commercial fisheries discard, with multiple items cut to act as bait for recreational fishing. Since the Mossel Bay harbour was thought to be a possible anthropogenic food source for these species, an acoustic receiver was deployed in this location. During the entire 2.5 year study period only four *Poroderma* individuals were detected inside the harbour, with the majority for less than 1.5 days. This might suggest that the harbour is not as an important source of anthropogenic food as initially suspected, that the majority of discarded bait is dumped outside of the harbour, or that due to the anthropogenic noise pollution as a result of boat engines, the listening power of the acoustic receiver was severely compromised. Additional research would be needed to confirm whether or not the harbour is an important anthropogenic food source for the two species.

The different temporal activity times seen between the two *Poroderma* spp. suggests differences in foraging behaviour and possibly feeding time (Woodland *et al.*, 2011). This distinction would be complementary with the difference in diet in relieving predation pressure of both *Poroderma* spp. on the ecosystem (Navia *et al.*, 2016), in particular cephalopods, as this food group was present in the diet of both species. The decline of any particular food group (either through stock collapse or other reasons) would likely not impact the *Poroderma* spp. as a whole, as is evident in the spatial variation in diet (Heupel *et al.*, 2014). In turn, the spatial variation in diet composition would lessen predation pressure on any single food group in a particular area, by having *Poroderma* spp. prey on different food sources throughout its range (Heupel *et al.*, 2014).

6.1.3 *Poroderma* spp. Along the Spatial Ecological Axis

To effectively implement management and conservation strategies on elasmobranchs, identifying the extent of movement and level of site fidelity is important (Henderson *et al.*, 2018; Elston *et al.*, 2021), even more so for species that occupy the same habitat. The space use in sympatric species has been examined in a variety marine predators (Jones *et al.*, 2015; Lea *et al.*, 2020; Elston *et al.*, 2021), including nearshore *Raja* spp. in the UK, showing fine-scale habitat segregation to reduce the effects of direct competition (Humphries *et al.*, 2016).

This study revealed that the movement behaviour of the *Poroderma* spp. was quite similar over a large spatial scale, as the minimum distance travelled from their initial tagging site and days at liberty were not significantly different between the two species. Visualization of the mark-recapture data also revealed that the movement distance for both species was consistent across the entire distribution range, suggesting a lack of subpopulations with varying movement behaviours. As their movement distance is relatively short, population genetics would be needed to explore the level of gene flow across the population range (Bester-van der Merwe

and Gledhill, 2015). This might elucidate the impact on population connectivity of the whole species in case localized populations are removed.

Passive acoustic telemetry in the Mossel Bay area revealed fine-scale variation in movement behaviour, with *P. africanum* showing more movement throughout the receiver array, while *P. pantherinum* showed higher residency. Residency was significantly correlated with depth, with both species being detected primarily on shallower receivers, and *P. pantherinum* showing no detections deeper than 35 m. There were more receivers deployed in shallower waters, with five of the eighteen receivers of the array were deployed deeper than 35 m. For both species, Cape St. Blaize was shown to be an area of high importance. As multiple reefs in the Mossel Bay area were covered by acoustic receivers, including on both sides of the receiver array, in addition to all the individuals having been tagged along the western side of the bay, this suggests that there is a degree of site-fidelity in both species.

Future studies should take habitat coverage into consideration. Both *Poroderma* spp. have been shown to be reef-associated species (de Vos *et al.*, 2015; Ebert *et al.*, 2021a), however, they are found on sand habitats as well, though in lower abundance (de Vos *et al.*, 2015). While the primary focus of the ichthyofaunal assemblage part of this study were the reef sites of Mossel Bay, passive acoustic telemetry revealed that both *Poroderma* spp. moved across the whole range of the acoustic array in Mossel Bay, this is supported by the stomach content analysis which showed an inclusion of sand-associated prey items.

The seasonal reduction in abundance of *P. africanum* during summer was not explained by the lateral movement along the coast. The majority of the conventional tagging data of the *Poroderma* spp. showed short lateral movement in both east-to-west and west-to-east directions throughout their range, while passive acoustic telemetry showed some inshore movement. Seasonal variation in abundance of *P. africanum* elsewhere along the coast (de Vos *et al.*, 2015) suggests this occurs throughout the range of the species. While individuals of *P. africanum*

travelled longer distances during the austral summer months, this was the minimum direct distance between two receivers, and did not account for diverging from this path. Additionally, the frequency that these individuals departed the detection range of acoustic receivers was not signficantly different during different times of the year. This suggests that during the austral summer months individual *P. africanum* either increase their foraging area, being away from their home reef for longer periods, or move offshore, leaving the area entirely, before returning inshore, potentially at neighbouring reefs.

Elasmobranchs are known to make seasonal offshore migrations (Domeier and Nasby-Lucas, 2008; Barnett and Semmens, 2012; Ketchum *et al.*, 2014), for example, *Squalus suckleyi* (Pacific spiny dogfish) in the North Pacific, which showed half-year absences from the Puget Sound, Washington, USA (Andrews and Harvey, 2013). Offshore movement of *P. africanum* is a possible explanation for the low presence of the species during the austral summer. While Juby (2016) identified *P. africanum* as being present in deep-aphotic areas (55–100 m depth) in Algoa Bay, South Africa, the study did not explore seasonality. Further examination of this would require the identification of offshore reefs sites, seasonal surveys of BRUVs to identify a contrasting pattern, and deployment of offshore receivers to confirm movement between inshore and offshore sites.

The distribution of many marine species are defined by thermal limits (Stuart-Smith *et al.*, 2017), and this is suggested to be the similar for both *Poroderma* spp., with the extreme temperatures on either side of southern Africa. The results of the BRUV deployments indicated that both species showed a higher probability of detection at lower temperatures (14–18 °C). This temperature range is consistent with the known distribution of the species, between 13 °C and 27 °C, with temperatures dropping below 13 °C along the west coast, and over 27 °C further along the east coast (Carr *et al.*, 2021).

Rouault *et al.* (2010) monitored SST along the South African coast between

1982 and 2009 and revealed an average decline of 0.5 °C per decade within the southern Benguela Current, a less intensive decline between Cape Agulhas and Plettenberg Bay, but an increase of up to 0.55 °C per decade within the Agulhas Current. This increases the gradient between the preferred temperature for the *Poroderma* spp. If the temperature continues to alter as a result of climatic changes, this can constrict the distribution ranges of *Poroderma* spp. as the fringes of the distribution would become more inhospitable for these species. This in turn can compromise the survivability of these species, or push the distribution to deeper waters (Dulvy *et al.*, 2008).

Analysis of movements from dart tagging data of *Poroderma* spp. revealed short lateral movement across its range. Movement analysis should be complemented with genetic stock assessments to understand the population connectivity across the species' range (Bester-van der Merwe and Gledhill, 2015). The presence of the Agulhas Current is thought to create an Indian/Atlantic Ocean boundary, limiting the gene flow across these areas (Teske *et al.*, 2013). This is evident in *M. mustelus* that showed strong genetic differentiation between the east and west of Cape Agulhas (Maduna *et al.*, 2016). *Poroderma* spp. display high site fidelity, sticking to home reefs, thus the extent of the effect of the Cape Agulhas boundary on the *Poroderma* spp. needs to be explored.

While the genetic structure of *P. pantherinum* has been explored (van Staden *et al.*, 2018), and the genetic distance between the two *Poroderma* spp. was determined (van Staden, 2018), no genetic stock assessment has been performed on either *Poroderma* spp. The genetic population structure of Scyliorhinidae has been explored elsewhere in the world and found strong differences between populations of *S. canicula* in the Mediterranean and Atlantic shelf (Gubili *et al.*, 2014). Genetic analysis should also explore the possibility of admixture within the genus (van Staden, 2018). While confusion in identification is not as problematic as in the

Haploblepharus genus (Human, 2007), there might be ontogenetic and geographic variation in the colour patterns and markings of *P. pantherinum* (Human, 2006b).

6.2 Coexistence and Conservation

The results of this study showed that the two sympatric species inhabited the area of Mossel Bay in coexistence rather than competing with one another, showing small niche differentiation amongst trophic and temporal ecological axes. Both species were seen on the BRUVs simultaneously, whereby no signs of intra- or interspecific aggression were noted, while the co-occurrence analysis indicated a positive co-occurrence between the two species. The stomach content showed a partial dietary niche overlap, whereby *P. africanum* was suggested to be a generalized predator, while *P. pantherinum* a specialized predator. These divergent dietary niches might be driven by the need to avoid competition between the two species. While competitive release, whereby changes in the relative abundance of sympatric carnivores can lead to an increase in the abundance or expansion of another species that directly competes with it for resources (Trewby *et al.*, 2008), might be a factor here, this would require further examination. As *P. africanum* is shown to be the generalist predator with wider movement behaviour, the effect of the declining yearly Relative Abundance of this species on the ecological behaviour of *P. pantherinum* is still to be seen. While similar locations within the study area were identified as important for both species, acoustic telemetry indicated temporal separation across daily timescales, while BRUVs showed temporal separation across seasonal time periods.

Small niche variation in sympatric species as seen in this study is similar to other sympatric mesopredators in other areas of the world (Vaudo and Heithaus, 2011; Humphries *et al.*, 2016; Elston *et al.*, 2021). For example in Shark Bay,

Western Australia, where the species of an inshore elasmobranch community showed various degrees of dietary overlap and differentiation, with *Himantura fai* (pink whipray) preferring a specialist diet consisting of *Penaeidae* spp. (penaeid shrimp), while *Glaucostegus typus* (common shovelnose ray) had a more diverse diet consisting of *Penaeidae*, crab and shrimp (Vaudo and Heithaus, 2011). Around the Hawaiian Islands four carcharhinid species showed niche differentiation along both spatial and trophic axes (Papastamatiou *et al.*, 2006). Outside chondrichthyan communities niche differentiation is seen across all taxa, such as mammals (e.g., primates: Oelze *et al.*, 2014; bats: Siemers and Schnitzler, 2004; carnivores: Jones and Barmuta, 2000), insects (Zimmermann *et al.*, 2009), and bacteria (Baran *et al.*, 2015).

Apart from size, the main physiological difference between the two species is their colour pattern, with *P. africanum* displaying long, horizontal stripes on a grey body, while *P. pantherinum* shows leopard-like rosettes to small or large black spots and partial longitudinal lines on a light to dark brown body (Compagno *et al.*, 2005). The differences in colour patterns can infer to be an extension of the ecological differences between the two species.

The colour patterns are primary indicators on how they might avoid predators, with the leopard-like rosettes of *P. pantherinum* suggesting blending in with their surroundings (i.e. background matching), while the longitudinal stripes of *P. africanum* suggests motion dazzle or disruptive colouration. While not part of this thesis, *P. pantherinum* amplified its camouflage pattern using its leopard-like rosettes with a freezing behaviour in response to the visual sightings of predators to avoid detection (Watson, R.G.A. pers. obs.). While this was also seen in the sympatric *Haploblepharus* spp., no information is available on anti-predatory response of *P. africanum*.

The colour pattern could have an impact on prey consumption, as it would

impact how the two species hunt. *Poroderma africanum* is a known ambush predator (Smale *et al.*, 1995, 2001), and its striped colouration could also be utilized to ambush prey by quickly closing the distance without the prey realizing. This explains the wide diversity of prey of *P. africanum*, as it could be utilized against a wide variety of prey. However, as it requires movement, it could also explain why the species does not reside at its home reef as long as *P. pantherinum*, and moves further throughout the area. *Poroderma pantherinum*'s background matching colouration would be more suitable for laying in wait and ambushing prey as they pass by. This would explain why the species is a more specialized predator towards a high energy-density prey, such as cephalopods.

The *Poroderma* spp. are not the only mesopredators in their ecosystem, and further investigation into the composition (and influence) of the food web would be necessary to get an idea of what the influence of a mesopredatory release would be on the assemblage. One way to achieve this would be through a large expansion on the BRUV work already performed in this study, with benthic BRUV deployments across all habitats and depth strata within the area of interest, complemented with pelagic BRUV (Mallet and Pelletier, 2014) deployments to account for mesopredators found higher in the water column. Further investigation would be required to determine whether *P. africanum* provides a concentrated predation risk on the ichthyofaunal assemblage within Mossel Bay, or is part of a suite of predators providing diffused predation risk (Heupel *et al.*, 2014). Combined with the life-history traits of both *Poroderma* spp., it is still unsure whether they would undergo the effects of mesopredatory release due to the removal of top predators, resulting in a trophic cascade (Heupel *et al.*, 2014).

During the course of the study both *Poroderma* spp. were downgraded on the IUCN Red List to Least Concerned , from Near Threatened and Data Deficient for

P. africanum and *P. pantherinum*, respectively (Pollom *et al.*, 2020a,b). The assessment was based on recreational catch data from the De Hoop Nature Reserve Marine Protected Area (MPA). Generation periods were 25 (Pollom *et al.*, 2020a) and 22 years (Pollom *et al.*, 2020b) for *P. africanum* and *P. pantherinum* respectively, while the MPA has been in place for 20 years (DEA 2020). As the populations had a generation of protection from exploitation, this explains the IUCN assessment showing an increase in population trend. However, this provides a skewed judgement of the actual population rates along the entire coastline, and the IUCN assessment might not be truly representative of the whole species across its entire distribution range. This is especially the case considering *P. africanum* showed a downward population trend, from 53 ± 52.05–56.82 (95%CI) to 16 ± 15.02–18.40 two years later, in a local population study in Mossel Bay (Grusd *et al.*, 2019), and a downward trend in seasonal relative abundance in this study. Considering these studies came out after the latest IUCN Red List assessments of the two *Poroderma* spp., the population trends of these species would need to be further assessed elsewhere around the South African coastline to determine whether these trends are consistent throughout their distributions.

In 2019, 20 new MPAs were declared in South Africa (DEA (Department of Environmental Affairs), 2019b), bringing the total up to 42, protecting approximately 5% of South Africa's Exclusive Economic Zone and covering 87% of different marine ecosystem types in South African waters (DEA 2019). The newly designated MPAs overlap 18.3% and 16.2% with *P. africanum* and *P. pantherinum* distribution ranges, respectively.

Conservation biologists and managers may focus conservation efforts on surrogate species in the hopes that it might benefit other species within the same ecosystem (Caro and O'Doherty, 1999). The 'umbrella species' concept focuses on habitat protection by aiming at one or a few species, which in turn would conserve co-occurring species that are of conservation concern (Caro and O'Doherty, 1999).

Another example of surrogacy is through the use of 'flagship species', whereby charismatic species are used to raise funds and public awareness to cover broader conservation targets (Caro and O'Doherty, 1999). For example, *Carcharodon carcharias* is used by various conservation NGOs around the world as a flagship species to promote conservation and research initiatives (Chivell, 2018; Apps *et al.*, 2018).

This leads to questions whether conservation and management plans of the *Poroderma* spp. should focus on a single species, the genus *Poroderma*, or whether *Poroderma* should be part of a broader umbrella species conservation complex (Osgood *et al.*, 2020). When multiple species occupy the same ecological niche, then a plan focusing on an umbrella/flagship species can be developed to protect the group as a whole without needlessly complicating management by developing plans for individual species. However, this would require that the management put in place would indeed cover all species within the conservation umbrella complex. Therefore the same information for all species under the 'umbrella' would need to be known. If a management plan for all inshore scyliorhinidae in South Africa would be developed, whether this would be on a local or national scale, ecological information should be collected for *Haploblepharus* spp., *Halaelurus* spp. and *Scyliorhinus capensis*.

The study suggests that the two *Poroderma* spp. are able to coexist within the same geographical area through niche differentiation across trophic and temporal ecological axes, with varying spatial use. The intra- and inter-specific differences between the two species may complicate elasmobranch management efforts for these co-occurring endemic scyliorhinidae, and as such, efforts should follow either an individual species approach, which is often not feasible, or an ecosystem-based approach, as opposed to considering the genus as a whole.

Several MPAs around South Africa are relatively small (Betty's Bay MPA: 4.5

km shoreline length; various no-take zones within the Table Mountain NP MPA: Boulders Restricted Zone: 2.7 km shoreline length; Castle Rock Restricted Zone: 2.8 km shoreline length; Paulsberg Restricted Zone: 2.2 km shoreline length, DEA (Department of Environmental Affairs) (2020)), or limited in their temporal scale (Walker Bay Whale Sanctuary open for six months out of the year). With the high site-fidelity of the *Poroderma* spp., and the movement shown to be frequently less than 10 km in radius as seen in both conventional tagging and acoustic telemetry data, protected areas should be large enough to cover, at minimum, the home range of the majority of the subpopulation to allow for the protection of the majority of the populations (Hooker *et al.*, 2011). Those that move great distances, thus spilling over from the protected area, would allow for genetic mixing of the species (Maggs *et al.*, 2013; Ward-Paige and Worm, 2017). MPAs such as the Goukamma MPA or Tsitsikamma MPA, with shoreline lengths of 16 km and 58 km, respectively, would be prime examples of protected areas adequate in size.

The habitat association of the *Poroderma* spp. would have an influence on the effectiveness of MPAs on their protection (Albano *et al.*, 2021). A study around Robberg MPA near Plettenberg Bay, Western Cape, South Africa, showed that *P. africanum* had a lower frequency of occurrence within the MPA compared to outside the MPA, which was likely due to the MPA covering a low amount of reef sites (Cortelezzi *et al.*, 2022). Therefore the effectiveness of established MPAs is dependent on whether the habitat it protects is associated with the species the MPA was designed for to protect.

Any spatial protection plans that would be implemented for the protection of *Poroderma* spp., or the *Poroderma* spp. within an umbrella species complex, should be large enough to cover the home ranges of the majority of a subpopulation, and the protection of the area should be enforced for over a *Poroderma*-generation to allow for the population to increase in abundance.

6.3 Conclusion

Scyliorhinidae are one of the largest elasmobranch families in the world and are widely represented within South Africa. Despite their diversity and abundance, the family as a whole is widely underexamined. This includes one of the morphologically larger scyliorhinidae genus' in South Africa, species of the *Poroderma* genus. The mesopredatory nature of these two species allowed for their coexistence within the Mossel Bay area, an anthropogenically impacted ecosystem. Partitioning of their ecology along temporal and trophic ecological axes was supported by fine-scale variation along the spatial ecological axis. This was evident in varying residency periods, differences in departure times, and movement across the receiver array from acoustic telemetry, partial resource overlap through gastric lavage, and seasonal varying Relative Abundances from *P. africanum* within the study area. Results from this study support the coexistence of these two species through the partitioning of their resources, thus allowing for coexistence in line with the theory of niche differentiation (Schoener, 1974).

Further research should corroborate the findings of this study elsewhere within the species' range, explore the genetic connectivity, and identify offshore seasonal behavioural patterns of both species. Home range analysis would inform the minimum potential size of MPAs that would be beneficial for the protection of the two species. With their position in the trophic web elucidated, and spatial variation in diet identified, population-wide stable isotope analysis to examine resource use patterns across the entire population would be an additional further step. These results, in comparison to data collected in protected areas, justifies the use of MPAs for the protection and conservation of these two species, and possibly scyliorhinidae as a whole. This research provides a stepping-stone towards further understanding scyliohinidae ecology within South Africa and adds vital knowledge

required for effective conservation and management concerns surrounding the *Poroderma* spp.

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Appendix A
Similarity Percentage (SIMPER) analyses

The following tables show the results of the Similarity Percentage (SIMPER) analyses on the fourth-root transformed fish community data between reefs (Tables A.1 to A.3), seasons (Table A.4), and quarters (Tables A.5 to A.10), with the species' cumulative contribution to the differences between categories shown up to 75%.

Table A.1: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between Darwin and Mitch reefs in Mossel Bay.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Fransmadam	0.05	0.03	1.49	1.85	0.77	0.09
Strepie	0.04	0.04	1.19	1.87	1.60	0.18
Olive grunter	0.03	0.03	1.15	0.63	1.03	0.25
Steentjie	0.03	0.03	1.19	1.11	1.91	0.32
Sand steenbras	0.03	0.02	1.13	0.71	0.79	0.37
Evileye pufferfish	0.02	0.02	1.10	0.64	0.14	0.42
Puffadder shyshark	0.02	0.02	1.06	0.41	0.69	0.46
Blacktail	0.02	0.02	0.86	1.47	1.86	0.50
Zebra	0.02	0.02	1.01	0.60	0.61	0.54
Twotone fingerfin	0.02	0.02	1.00	0.55	0.34	0.58
Pyjama catshark	0.02	0.02	0.96	0.48	0.36	0.62
Octopus	0.02	0.02	0.91	0.25	0.46	0.65
Santer	0.02	0.02	0.87	0.29	0.40	0.69
Super klipfish	0.01	0.02	0.79	0.19	0.35	0.72
Red roman	0.01	0.02	0.70	1.36	1.14	0.74
Leopard catshark	0.01	0.02	0.63	0.18	0.20	0.77

Table A.2: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between Darwin and Roman's reefs in Mossel Bay.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.04	0.04	1.22	1.87	1.57	0.09
Fransmadam	0.04	0.03	1.42	1.85	0.88	0.18
Steentjie	0.04	0.03	1.27	1.11	2.01	0.26
Olive grunter	0.03	0.03	1.07	0.63	0.88	0.32
Sand steenbras	0.02	0.02	1.12	0.71	0.59	0.37
Evileye pufferfish	0.02	0.02	1.11	0.64	0.08	0.41
Santer	0.02	0.02	1.12	0.29	0.69	0.45
Twotone fingerfin	0.02	0.02	1.03	0.55	0.53	0.50
Puffadder shyshark	0.02	0.02	1.01	0.41	0.62	0.54
Zebra	0.02	0.02	1.00	0.60	0.63	0.57
Blacktail	0.02	0.02	0.84	1.47	1.77	0.61
Pyjama catshark	0.02	0.02	0.95	0.48	0.39	0.65
Octopus	0.02	0.02	0.92	0.25	0.49	0.69
Super klipfish	0.01	0.02	0.77	0.19	0.33	0.71
Doublesash butterflyfish	0.01	0.02	0.68	0.18	0.25	0.74
Leopard catshark	0.01	0.02	0.59	0.18	0.16	0.76
John Brown	0.01	0.02	0.60	0.10	0.23	0.78

Table A.3: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between Mitch and Roman's reefs in Mossel Bay.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.04	0.03	1.21	1.60	1.57	0.09
Olive grunter	0.04	0.03	1.18	1.03	0.88	0.18
Fransmadam	0.03	0.02	1.18	0.77	0.88	0.25
Sand steenbras	0.02	0.02	1.10	0.79	0.59	0.30
Steentjie	0.02	0.03	0.85	1.91	2.01	0.36
Santer	0.02	0.02	1.13	0.40	0.69	0.41
Zebra	0.02	0.02	1.01	0.61	0.63	0.46
Octopus	0.02	0.02	0.98	0.46	0.49	0.50
Twotone fingerfin	0.02	0.02	1.00	0.34	0.53	0.55
Pyjama catshark	0.02	0.02	0.91	0.36	0.39	0.59
Puffadder shyshark	0.02	0.02	0.95	0.69	0.62	0.63
Super klipfish	0.02	0.02	0.86	0.35	0.33	0.67
Blacktail	0.01	0.02	0.88	1.86	1.77	0.70
Doublesash butterflyfish	0.01	0.02	0.71	0.21	0.25	0.73
Red roman	0.01	0.02	0.72	1.14	1.34	0.76
Leopard catshark	0.01	0.02	0.61	0.20	0.16	0.78

Table A.4: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between summer and winter.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.04	0.04	1.25	1.38	1.98	0.09
Olive grunter	0.04	0.03	1.30	0.44	1.24	0.18
Fransmadam	0.04	0.03	1.34	0.83	1.52	0.26
Steentjie	0.03	0.03	1.07	1.55	1.78	0.32
Sand steenbras	0.03	0.02	1.21	0.50	0.89	0.37
Santer	0.02	0.02	1.10	0.25	0.67	0.42
Zebra	0.02	0.02	1.10	0.46	0.77	0.46
Twotone fingerfin	0.02	0.02	1.08	0.33	0.62	0.50
Puffadder shyshark	0.02	0.02	1.05	0.69	0.45	0.54
Pyjama catshark	0.02	0.02	0.99	0.53	0.30	0.58
Octopus	0.02	0.02	0.93	0.39	0.40	0.62
Blacktail	0.02	0.02	0.87	1.61	1.78	0.66
Evileye pufferfish	0.02	0.02	0.83	0.19	0.40	0.69
Super klipfish	0.01	0.02	0.81	0.28	0.29	0.72
Doublesash butterflyfish	0.01	0.02	0.72	0.08	0.34	0.74
Leopard catshark	0.01	0.02	0.63	0.23	0.13	0.76

Table A.5: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 1 and 2.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Olive grunter	0.04	0.03	1.37	1.43	0.66	0.09
Strepie	0.04	0.03	1.18	2.08	1.53	0.17
Fransmadam	0.03	0.02	1.24	1.74	1.18	0.23
Sand steenbras	0.02	0.02	1.20	0.82	0.42	0.29
Santer	0.02	0.02	1.24	0.89	0.36	0.34
Steentjie	0.02	0.02	1.12	1.81	1.77	0.38
Puffadder shyshark	0.02	0.02	1.12	0.30	0.68	0.42
Zebra	0.02	0.02	1.06	0.85	0.53	0.47
Twotone fingerfin	0.02	0.02	1.10	0.64	0.30	0.51
Pyjama catshark	0.02	0.02	1.02	0.29	0.55	0.55
Blacktail	0.02	0.02	0.84	1.81	1.63	0.59
Octopus	0.02	0.02	0.98	0.51	0.40	0.63
Evileye pufferfish	0.02	0.02	0.90	0.46	0.20	0.66
Doublesash butterflyfish	0.01	0.02	0.91	0.46	0.14	0.70
Carpenter	0.01	0.02	0.65	0.39	0.06	0.72
Super klipfish	0.01	0.02	0.76	0.21	0.30	0.75

Table A.6: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 1 and 3.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.05	0.04	1.40	1.22	2.08	0.09
Fransmadam	0.05	0.03	1.78	0.44	1.74	0.19
Olive grunter	0.05	0.03	1.49	0.21	1.43	0.28
Steentjie	0.03	0.03	1.17	1.31	1.81	0.34
Santer	0.03	0.02	1.53	0.13	0.89	0.39
Sand steenbras	0.02	0.02	1.15	0.58	0.82	0.44
Zebra	0.02	0.02	1.22	0.38	0.85	0.49
Puffadder shyshark	0.02	0.02	1.11	0.70	0.30	0.53
Twotone fingerfin	0.02	0.02	1.11	0.35	0.64	0.57
Octopus	0.02	0.02	0.98	0.38	0.51	0.60
Pyjama catshark	0.02	0.02	0.96	0.50	0.29	0.64
Blacktail	0.02	0.02	0.81	1.59	1.81	0.67
Evileye pufferfish	0.02	0.02	0.88	0.18	0.46	0.70
Doublesash butterflyfish	0.02	0.02	0.87	0.02	0.46	0.73
Carpenter	0.01	0.02	0.62	0.03	0.39	0.76
Super klipfish	0.01	0.02	0.72	0.26	0.21	0.78

Table A.7: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 1 and 4.

Species	average	sd	ratio	ava	avb	cumsum
Olive grunter	0.03	0.02	1.27	1.43	1.00	0.08
Strepie	0.03	0.03	1.19	2.08	1.87	0.15
Fransmadam	0.03	0.02	1.31	1.74	1.26	0.23
Santer	0.02	0.02	1.30	0.89	0.40	0.28
Sand steenbras	0.02	0.02	1.09	0.82	0.97	0.33
Puffadder shyshark	0.02	0.02	1.07	0.30	0.63	0.37
Twotone fingerfin	0.02	0.02	1.06	0.64	0.60	0.41
Steentjie	0.02	0.02	1.10	1.81	1.75	0.46
Octopus	0.02	0.02	1.00	0.51	0.28	0.50
Zebra	0.02	0.02	0.94	0.85	0.67	0.53
Evileye pufferfish	0.02	0.02	0.93	0.46	0.31	0.57
Doublesash butterflyfish	0.01	0.02	0.92	0.46	0.18	0.61
Super klipfish	0.01	0.02	0.87	0.21	0.40	0.64
Blacktail	0.01	0.01	0.92	1.81	1.75	0.67
Pyjama catshark	0.01	0.02	0.82	0.29	0.30	0.70
Carpenter	0.01	0.02	0.66	0.39	0.07	0.73

Table A.8: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 2 and 3.

Species	average	sd	ratio	ava	avb	cumsum
Strepie	0.05	0.04	1.31	1.22	1.53	0.11
Fransmadam	0.04	0.03	1.31	0.44	1.18	0.19
Steentjie	0.04	0.04	1.15	1.31	1.77	0.28
Olive grunter	0.03	0.04	0.83	0.21	0.66	0.34
Sand steenbras	0.03	0.02	1.04	0.58	0.42	0.39
Pyjama catshark	0.02	0.02	1.02	0.50	0.55	0.44
Zebra	0.02	0.02	1.00	0.38	0.53	0.48
Blacktail	0.02	0.03	0.84	1.59	1.63	0.53
Octopus	0.02	0.02	0.92	0.38	0.40	0.57
Puffadder shyshark	0.02	0.02	0.91	0.70	0.68	0.61
Twotone fingerfin	0.02	0.02	0.85	0.35	0.30	0.64
Super klipfish	0.02	0.02	0.80	0.26	0.30	0.68
Santer	0.02	0.02	0.78	0.13	0.36	0.71
Leopard catshark	0.01	0.02	0.72	0.26	0.20	0.74
Evileye pufferfish	0.01	0.02	0.63	0.18	0.20	0.77
White steenbras	0.01	0.02	0.57	0.06	0.26	0.79

Table A.9: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 2 and 4.

Species	average	sd	ratio	ava	avb	cumsum
Strepie	0.04	0.03	1.24	1.53	1.87	0.09
Fransmadam	0.03	0.03	1.28	1.18	1.26	0.17
Olive grunter	0.03	0.03	1.22	0.66	1.00	0.25
Sand steenbras	0.03	0.02	1.33	0.42	0.97	0.31
Steentjie	0.02	0.02	1.10	1.77	1.75	0.36
Twotone fingerfin	0.02	0.02	1.06	0.30	0.60	0.41
Pyjama catshark	0.02	0.02	1.02	0.55	0.30	0.45
Zebra	0.02	0.02	1.04	0.53	0.67	0.49
Puffadder shyshark	0.02	0.02	0.98	0.68	0.63	0.53
Santer	0.02	0.02	0.93	0.36	0.40	0.57
Blacktail	0.02	0.02	0.93	1.63	1.75	0.61
Super klipfish	0.02	0.02	0.90	0.30	0.40	0.65
Octopus	0.02	0.02	0.90	0.40	0.28	0.68
Evileye pufferfish	0.01	0.02	0.77	0.20	0.31	0.71
Leopard catshark	0.01	0.02	0.61	0.20	0.14	0.74
John Brown	0.01	0.02	0.61	0.06	0.25	0.76

Table A.10: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between quarter 3 and 4.

Species	average	sd	ratio	ava	avb	cumsum
Strepie	0.05	0.04	1.31	1.22	1.87	0.11
Fransmadam	0.04	0.03	1.28	0.44	1.26	0.19
Steentjie	0.04	0.03	1.18	1.31	1.75	0.27
Olive grunter	0.04	0.03	1.16	0.21	1.00	0.35
Sand steenbras	0.03	0.02	1.19	0.58	0.97	0.40
Zebra	0.02	0.02	1.10	0.38	0.67	0.45
Twotone fingerfin	0.02	0.02	1.07	0.35	0.60	0.49
Pyjama catshark	0.02	0.02	0.97	0.50	0.30	0.54
Puffadder shyshark	0.02	0.02	0.98	0.70	0.63	0.58
Octopus	0.02	0.02	0.86	0.38	0.28	0.61
Super klipfish	0.02	0.02	0.88	0.26	0.40	0.65
Blacktail	0.02	0.02	0.94	1.59	1.75	0.68
Santer	0.02	0.02	0.79	0.13	0.40	0.71
Evileye pufferfish	0.01	0.02	0.75	0.18	0.31	0.74
John Brown	0.01	0.02	0.73	0.22	0.25	0.77
Leopard catshark	0.01	0.02	0.68	0.26	0.14	0.80

Table A.11: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2015 and 2016.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.05	0.04	1.07	2.12	1.67	0.10
Fransmadam	0.03	0.03	1.16	0.66	0.90	0.18
Steentjie	0.03	0.03	1.12	1.49	1.58	0.25
Red roman	0.02	0.03	0.91	0.98	1.30	0.30
Pyjama catshark	0.02	0.02	1.09	0.70	0.45	0.35
Octopus	0.02	0.02	0.98	0.55	0.28	0.40
Olive grunter	0.02	0.03	0.81	0.33	0.46	0.44
Zebra	0.02	0.02	1.00	0.70	0.61	0.49
Sand steenbras	0.02	0.02	0.90	0.17	0.51	0.53
Puffadder shyshark	0.02	0.02	0.96	0.70	0.69	0.57
Santer	0.02	0.02	0.86	0.40	0.27	0.61
Twotone fingerfin	0.02	0.02	0.93	0.33	0.44	0.65
Super klipfish	0.02	0.02	0.82	0.17	0.38	0.69
Evileye pufferfish	0.02	0.02	0.82	0.33	0.28	0.72
Blacktail	0.02	0.01	1.15	1.66	1.77	0.76

Table A.12: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2015 and 2017.

Species	**average**	**sd**	**ratio**	**ava**	**avb**	**cumsum**
Strepie	0.05	0.04	1.17	2.12	1.56	0.10
Fransmadam	0.04	0.03	1.30	0.66	1.30	0.18
Olive grunter	0.03	0.03	1.09	0.33	0.96	0.25
Steentjie	0.03	0.03	1.02	1.49	1.70	0.31
Sand steenbras	0.03	0.02	1.23	0.17	0.83	0.37
Red roman	0.02	0.03	0.94	0.98	1.28	0.42
Pyjama catshark	0.02	0.02	1.06	0.70	0.40	0.47
Octopus	0.02	0.02	0.99	0.55	0.46	0.52
Santer	0.02	0.02	1.04	0.40	0.53	0.56
Zebra	0.02	0.02	1.01	0.70	0.57	0.60
Puffadder shyshark	0.02	0.02	1.01	0.70	0.50	0.65
Blacktail	0.02	0.02	0.87	1.66	1.63	0.69
Twotone fingerfin	0.02	0.02	0.95	0.33	0.48	0.72
Evileye pufferfish	0.02	0.02	0.81	0.33	0.26	0.76

Table A.13: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2015 and 2018.

Species	average	sd	ratio	ava	avb	cumsum
Olive grunter	0.05	0.03	1.68	0.33	1.76	0.11
Fransmadam	0.04	0.03	1.43	0.66	1.72	0.19
Strepie	0.03	0.03	1.15	2.12	2.11	0.26
Sand steenbras	0.03	0.02	1.34	0.17	0.92	0.32
Santer	0.02	0.02	1.30	0.40	0.81	0.37
Steentjie	0.02	0.02	0.95	1.49	1.87	0.42
Pyjama catshark	0.02	0.02	1.17	0.70	0.27	0.46
Red roman	0.02	0.02	0.96	0.98	1.29	0.50
Carpenter	0.02	0.02	0.81	0.00	0.59	0.54
Octopus	0.02	0.02	1.03	0.55	0.45	0.58
Puffadder shyshark	0.02	0.02	1.06	0.70	0.44	0.62
Twotone fingerfin	0.02	0.02	1.09	0.33	0.63	0.66
Evileye pufferfish	0.02	0.02	0.92	0.33	0.44	0.70
Zebra	0.02	0.02	0.90	0.70	0.81	0.73
Doublesash butterflyfish	0.01	0.02	0.87	0.20	0.41	0.76

Table A.14: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2016 and 2017.

Species	average	sd	ratio	ava	avb	cumsum
Strepie	0.04	0.04	1.22	1.67	1.56	0.09
Fransmadam	0.04	0.03	1.30	0.90	1.30	0.17
Olive grunter	0.03	0.03	1.12	0.46	0.96	0.25
Steentjie	0.03	0.03	1.04	1.58	1.70	0.31
Sand steenbras	0.03	0.02	1.15	0.51	0.83	0.37
Zebra	0.02	0.02	1.02	0.61	0.57	0.41
Puffadder shyshark	0.02	0.02	1.00	0.69	0.50	0.45
Santer	0.02	0.02	1.00	0.27	0.53	0.49
Twotone fingerfin	0.02	0.02	0.99	0.44	0.48	0.53
Pyjama catshark	0.02	0.02	0.94	0.45	0.40	0.58
Blacktail	0.02	0.02	0.84	1.77	1.63	0.62
Octopus	0.02	0.02	0.93	0.28	0.46	0.65
Super klipfish	0.02	0.02	0.83	0.38	0.20	0.69
Evileye pufferfish	0.01	0.02	0.76	0.28	0.26	0.72
Leopard catshark	0.01	0.02	0.62	0.19	0.17	0.74
Red roman	0.01	0.01	0.70	1.30	1.28	0.76

Table A.15: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2016 and 2018.

Species	average	sd	ratio	ava	avb	cumsum
Olive grunter	0.05	0.03	1.70	0.46	1.76	0.10
Fransmadam	0.04	0.03	1.41	0.90	1.72	0.19
Strepie	0.04	0.03	1.20	1.67	2.11	0.27
Sand steenbras	0.02	0.02	1.19	0.51	0.92	0.32
Santer	0.02	0.02	1.34	0.27	0.81	0.37
Steentjie	0.02	0.02	1.09	1.58	1.87	0.41
Carpenter	0.02	0.02	0.82	0.02	0.59	0.46
Twotone fingerfin	0.02	0.02	1.09	0.44	0.63	0.50
Puffadder shyshark	0.02	0.02	1.06	0.69	0.44	0.54
Zebra	0.02	0.02	0.98	0.61	0.81	0.57
Pyjama catshark	0.02	0.02	0.92	0.45	0.27	0.61
Octopus	0.02	0.02	0.94	0.28	0.45	0.64
Evileye pufferfish	0.02	0.02	0.91	0.28	0.44	0.68
Super klipfish	0.01	0.02	0.92	0.38	0.36	0.71
Doublesash butterflyfish	0.01	0.02	0.85	0.16	0.41	0.74
Blacktail	0.01	0.01	1.28	1.77	1.75	0.76

Table A.16: The results of a Similarity Percentage (SIMPER) analysis performed on the population composition of the BRUV deployments between year 2017 and 2018.

Species	average	sd	ratio	ava	avb	cumsum
Olive grunter	0.04	0.03	1.29	0.96	1.76	0.09
Strepie	0.04	0.03	1.19	1.56	2.11	0.18
Fransmadam	0.03	0.02	1.16	1.30	1.72	0.24
Sand steenbras	0.02	0.02	1.10	0.83	0.92	0.30
Steentjie	0.02	0.02	0.95	1.70	1.87	0.34
Carpenter	0.02	0.02	0.85	0.14	0.59	0.39
Santer	0.02	0.02	1.08	0.53	0.81	0.43
Twotone fingerfin	0.02	0.02	1.08	0.48	0.63	0.48
Zebra	0.02	0.02	1.03	0.57	0.81	0.52
Octopus	0.02	0.02	0.98	0.46	0.45	0.56
Puffadder shyshark	0.02	0.02	0.98	0.50	0.44	0.60
Evileye pufferfish	0.02	0.02	0.91	0.26	0.44	0.63
Pyjama catshark	0.01	0.02	0.88	0.40	0.27	0.67
Blacktail	0.01	0.02	0.80	1.63	1.75	0.70
Doublesash butterflyfish	0.01	0.02	0.87	0.21	0.41	0.73
Super klipfish	0.01	0.02	0.81	0.20	0.36	0.76

Appendix B
Binomial Regression Model Variations

The following tables show model-variations for the binomial regression analyses of environmental parameters for the presence/absence of *P. africanum* (Table B.1) and *P. pantherinum* (Table B.2). The tables were generated using the `dredge`-function of the `MuMIn` package, and ordered according to increasing AIC values.

Table B.1: Binomial regression model variations of *P. africanum* presence/absence against environmental parameters.

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
2.68		0.01			-0.24	0.66				4	-112.53	233.29	0.00	0.06
2.88					-0.23	0.62				3	-113.76	233.65	0.35	0.05
1.94	0.16	0.01			-0.25	0.67				5	-111.71	233.75	0.46	0.05
2.21	0.14				-0.24	0.62				4	-113.07	234.36	1.06	0.04
2.62		0.01		6.54	-0.24	0.68				5	-112.21	234.75	1.46	0.03
2.37		0.01			-0.24	0.89			-0.00	5	-112.27	234.87	1.58	0.03
1.54	0.17	0.01			-0.25	0.95			-0.01	6	-111.33	235.13	1.84	0.03
15.42		0.01	-0.01		-0.25	0.64				5	-112.47	235.28	1.99	0.02
1.90	0.16	0.01		6.17	-0.25	0.69				6	-111.41	235.30	2.00	0.02
2.85				4.77	-0.23	0.63				4	-113.57	235.36	2.07	0.02
2.71		0.01			-0.24	0.66	-0.02			5	-112.51	235.37	2.08	0.02
2.75		0.01			-0.24	0.65		-0.00		5	-112.52	235.37	2.08	0.02
14.15			-0.01		-0.24	0.60				4	-113.71	235.64	2.34	0.02
2.91					-0.23	0.62	-0.02			4	-113.74	235.71	2.42	0.02
2.90					-0.23	0.61		-0.00		4	-113.76	235.74	2.44	0.02
10.94	0.16	0.01	-0.01		-0.26	0.66				6	-111.68	235.83	2.54	0.02
1.97	0.16	0.01			-0.25	0.67	-0.02			6	-111.69	235.85	2.56	0.02
2.00	0.16	0.01			-0.25	0.66		-0.00		6	-111.70	235.87	2.58	0.02
2.23		0.01		7.66	-0.24	0.97			-0.01	6	-111.84	236.16	2.86	0.02
2.20	0.14			4.34	-0.24	0.64				5	-112.91	236.16	2.86	0.02
10.23	0.14		-0.01		-0.24	0.61				5	-113.04	236.42	3.13	0.01
2.24	0.14				-0.23	0.62	-0.02			5	-113.05	236.45	3.15	0.01
2.21	0.14				-0.24	0.62		0.00		5	-113.07	236.47	3.18	0.01
1.41	0.17	0.02		7.45	-0.25	1.03			-0.01	7	-110.92	236.48	3.18	0.01
20.44		0.01	-0.02		-0.26	0.90			-0.00	6	-112.14	236.76	3.47	0.01
12.47		0.01	-0.01	6.32	-0.25	0.67				6	-112.17	236.82	3.52	0.01
2.66		0.01		6.59	-0.24	0.69	-0.03			6	-112.18	236.83	3.54	0.01
2.69		0.01		6.48	-0.24	0.68		-0.00		6	-112.19	236.86	3.57	0.01
2.42		0.01			-0.24	0.88		-0.00	-0.00	6	-112.26	237.00	3.70	0.01
2.39		0.01			-0.24	0.89	-0.01		-0.00	6	-112.26	237.00	3.71	0.01
16.32	0.17	0.02	-0.01		-0.26	0.96			-0.01	7	-111.25	237.13	3.84	0.01
1.56	0.17	0.01			-0.25	0.95		-0.00	-0.01	7	-111.33	237.29	4.00	0.01
1.54	0.17	0.01			-0.25	0.95	-0.00		-0.01	7	-111.33	237.29	4.00	0.01
15.85		0.01	-0.01		-0.25	0.64	-0.02			6	-112.45	237.37	4.08	0.01
16.06		0.01	-0.01		-0.25	0.63		-0.00		6	-112.45	237.37	4.08	0.01
1.94	0.16	0.01		6.22	-0.25	0.70	-0.02			7	-111.38	237.40	4.11	0.01
11.90			-0.01	4.56	-0.24	0.62				5	-113.54	237.41	4.12	0.01
8.10	0.16	0.01	-0.01	6.03	-0.26	0.69				7	-111.40	237.43	4.14	0.01
2.89				4.80	-0.23	0.64	-0.02			5	-113.55	237.44	4.14	0.01
1.96	0.16	0.01		6.12	-0.25	0.69		-0.00		7	-111.40	237.44	4.15	0.01
2.86				4.76	-0.23	0.63		-0.00		5	-113.57	237.48	4.19	0.01
2.74		0.01			-0.24	0.65	-0.01	-0.00		6	-112.51	237.50	4.20	0.01
14.51			-0.01		-0.24	0.60	-0.02			5	-113.69	237.72	4.42	0.01
14.28			-0.01		-0.24	0.60		-0.00		5	-113.70	237.75	4.46	0.01
2.89					-0.23	0.62	-0.02	0.00		5	-113.74	237.82	4.53	0.01
11.38	0.16	0.01	-0.01		-0.26	0.66	-0.02			7	-111.65	237.95	4.66	0.01
11.47	0.16	0.01	-0.01		-0.26	0.65		-0.00		7	-111.66	237.96	4.67	0.01
2.00	0.16	0.01			-0.25	0.67	-0.02	-0.00		7	-111.69	238.01	4.72	0.01
17.80		0.02	-0.02	7.41	-0.26	0.97			-0.01	7	-111.75	238.14	4.84	0.01
2.23	0.14			4.37	-0.23	0.64	-0.02			6	-112.89	238.26	4.97	0.01
8.18	0.14		-0.01	4.21	-0.24	0.63				6	-112.89	238.27	4.97	0.01
2.19	0.14			4.35	-0.24	0.64		0.00		6	-112.91	238.29	5.00	0.01
2.26		0.01		7.66	-0.24	0.96	-0.01		-0.01	7	-111.83	238.30	5.01	0.01
2.28		0.01		7.62	-0.24	0.96		-0.00	-0.01	7	-111.83	238.31	5.02	0.01
2.85					-0.19					2	-117.12	238.31	5.02	0.01
10.58	0.14		-0.01		-0.24	0.61	-0.02			6	-113.03	238.53	5.24	0.00
13.68	0.17	0.02	-0.01	7.25	-0.26	1.03			-0.01	8	-110.86	238.55	5.26	0.00
10.24	0.14		-0.01		-0.24	0.61		-0.00		6	-113.04	238.56	5.27	0.00
2.20	0.14				-0.23	0.63	-0.02	0.00		6	-113.05	238.57	5.28	0.00
1.43	0.17	0.02		7.44	-0.25	1.02	-0.01		-0.01	8	-110.92	238.66	5.37	0.00
1.43	0.17	0.02		7.43	-0.25	1.02		-0.00	-0.01	8	-110.92	238.66	5.37	0.00
2.68		0.01			-0.19					3	-116.29	238.71	5.42	0.00
20.82		0.01	-0.02		-0.26	0.89		-0.00	-0.00	7	-112.13	238.90	5.61	0.00
12.93		0.01	-0.01	6.36	-0.25	0.67	-0.03			7	-112.13	238.91	5.62	0.00
20.51		0.01	-0.02		-0.26	0.90	-0.01		-0.00	7	-112.14	238.92	5.62	0.00
13.07		0.01	-0.01	6.24	-0.25	0.66		-0.00		7	-112.15	238.94	5.65	0.00
2.68		0.01		6.56	-0.24	0.68	-0.02	-0.00		7	-112.17	238.99	5.69	0.00
2.19	0.14				-0.19					3	-116.45	239.04	5.75	0.00
2.42		0.01			-0.24	0.88	-0.00	-0.00	-0.00	7	-112.26	239.16	5.87	0.00
1.96	0.15	0.01			-0.20					4	-115.53	239.28	5.99	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
16.55	0.17	0.02	-0.01		-0.26	0.95		-0.00	-0.01	8	-111.24	239.31	6.02	0.00
16.36	0.17	0.02	-0.01		-0.26	0.95	-0.00		-0.01	8	-111.25	239.32	6.03	0.00
1.56	0.17	0.01			-0.25	0.95	-0.00	-0.00	-0.01	8	-111.33	239.48	6.19	0.00
12.27			-0.01	4.59	-0.24	0.62	-0.02			6	-113.51	239.51	6.21	0.00
16.13		0.01	-0.01		-0.25	0.63	-0.01	-0.00		7	-112.44	239.52	6.23	0.00
11.98			-0.01	4.55	-0.24	0.62		-0.00		6	-113.54	239.55	6.26	0.00
8.57	0.16	0.01	-0.01	6.08	-0.25	0.69	-0.03			8	-111.36	239.56	6.26	0.00
2.85				4.86	-0.23	0.64	-0.03	0.00		6	-113.54	239.56	6.27	0.00
1.95	0.16	0.01		6.21	-0.25	0.70	-0.02	-0.00		8	-111.38	239.59	6.30	0.00
8.59	0.15	0.01	-0.01	5.98	-0.26	0.68		-0.00		8	-111.38	239.59	6.30	0.00
30.41			-0.03		-0.21					3	-116.80	239.73	6.43	0.00
14.44			-0.01		-0.24	0.60	-0.02	0.00		6	-113.69	239.85	6.56	0.00
33.07		0.01	-0.03		-0.22					4	-115.90	240.02	6.72	0.00
3.07					-0.19			-0.00		3	-116.96	240.06	6.77	0.00
11.56	0.16	0.01	-0.01		-0.26	0.65	-0.02	-0.00		8	-111.65	240.13	6.84	0.00
2.84				2.26	-0.19					3	-117.08	240.29	7.00	0.00
2.95		0.01			-0.20			-0.00		4	-116.04	240.30	7.01	0.00
18.14		0.02	-0.02	7.35	-0.26	0.96		-0.00	-0.01	8	-111.74	240.31	7.02	0.00
17.90		0.02	-0.02	7.41	-0.26	0.97	-0.01		-0.01	8	-111.74	240.31	7.02	0.00
2.87					-0.19		-0.01			3	-117.12	240.37	7.07	0.00
8.54	0.14		-0.01	4.24	-0.24	0.63	-0.02			7	-112.88	240.39	7.10	0.00
2.17	0.14			4.46	-0.23	0.65	-0.03	0.00		7	-112.88	240.40	7.11	0.00
8.12	0.14		-0.01	4.22	-0.24	0.63		0.00		7	-112.89	240.43	7.14	0.00
2.28		0.01		7.64	-0.24	0.96	-0.01	-0.00	-0.01	8	-111.83	240.49	7.20	0.00
2.65		0.01		3.51	-0.19					4	-116.18	240.59	7.30	0.00
26.67	0.13		-0.02		-0.21					4	-116.20	240.63	7.33	0.00
10.41	0.14		-0.01		-0.24	0.62	-0.02	0.00		7	-113.02	240.68	7.39	0.00
13.76	0.17	0.02	-0.01	7.25	-0.26	1.02	-0.01		-0.01	9	-110.86	240.76	7.47	0.00
13.86	0.17	0.02	-0.01	7.22	-0.26	1.02		-0.00	-0.01	9	-110.86	240.76	7.47	0.00
29.19	0.14	0.01	-0.03		-0.22					5	-115.22	240.78	7.49	0.00
2.70		0.01			-0.19		-0.01			4	-116.28	240.78	7.49	0.00
2.40	0.14				-0.19			-0.00		4	-116.32	240.86	7.57	0.00
1.43	0.17	0.02		7.44	-0.25	1.02	-0.01	-0.00	-0.01	9	-110.92	240.87	7.58	0.00
2.23	0.15	0.01			-0.20			-0.00		5	-115.30	240.94	7.65	0.00
2.18	0.14			1.83	-0.19					4	-116.42	241.07	7.78	0.00
20.81		0.01	-0.02		-0.26	0.89	-0.00	-0.00	-0.00	8	-112.13	241.09	7.80	0.00
13.12		0.01	-0.01	6.32	-0.25	0.67	-0.02	-0.00		8	-112.13	241.09	7.80	0.00
2.20	0.14				-0.19		-0.01			4	-116.45	241.12	7.83	0.00
1.94	0.15	0.01		3.11	-0.20					5	-115.44	241.23	7.94	0.00
1.98	0.15	0.01			-0.20		-0.01			5	-115.52	241.39	8.09	0.00
31.03			-0.03		-0.22			-0.00		4	-116.63	241.48	8.19	0.00
16.55	0.17	0.02	-0.01		-0.26	0.95	-0.00	-0.00	-0.01	9	-111.24	241.53	8.23	0.00
34.08		0.01	-0.03		-0.23			-0.00		5	-115.63	241.60	8.30	0.00
12.09			-0.01	4.65	-0.24	0.63	-0.03	0.00		7	-113.51	241.66	8.37	0.00
29.75			-0.03	1.80	-0.21					4	-116.77	241.76	8.47	0.00
8.66	0.16	0.01	-0.01	6.06	-0.25	0.69	-0.02	-0.00		9	-111.36	241.77	8.47	0.00
30.72			-0.03		-0.21		-0.02			4	-116.78	241.79	8.50	0.00
32.06		0.01	-0.03	3.05	-0.22					5	-115.82	241.98	8.68	0.00
3.06				2.14	-0.19			-0.00		4	-116.92	242.07	8.78	0.00
33.39		0.01	-0.03		-0.22		-0.02			5	-115.88	242.10	8.81	0.00
3.08					-0.19		0.02	-0.00		4	-116.95	242.13	8.83	0.00
2.92		0.01		3.42	-0.20			-0.00		5	-115.93	242.21	8.91	0.00
2.95		0.01			-0.20		0.03	-0.00		5	-116.01	242.35	9.06	0.00
2.86				2.28	-0.19		-0.01			4	-117.07	242.36	9.07	0.00
30.22	0.14	0.01	-0.03		-0.23			-0.00		6	-114.98	242.43	9.14	0.00
27.31	0.13		-0.02		-0.22			-0.00		5	-116.06	242.45	9.16	0.00
18.10		0.02	-0.02	7.37	-0.26	0.96	-0.01	-0.00	-0.01	9	-111.74	242.52	9.22	0.00
8.27	0.14		-0.01	4.32	-0.24	0.64	-0.03	0.00		8	-112.87	242.56	9.27	0.00
2.68		0.01		3.53	-0.19		-0.02			5	-116.17	242.68	9.39	0.00
26.16	0.13		-0.02	1.44	-0.21					5	-116.18	242.70	9.41	0.00
26.94	0.13		-0.02		-0.21		-0.01			5	-116.19	242.72	9.43	0.00
28.31	0.14	0.01	-0.03	2.72	-0.22					6	-115.16	242.79	9.50	0.00
29.48	0.14	0.01	-0.03		-0.22		-0.01			6	-115.21	242.90	9.60	0.00
2.21	0.15	0.01		3.03	-0.20			-0.00		6	-115.22	242.92	9.62	0.00
2.40	0.14			1.72	-0.19			-0.00		5	-116.29	242.92	9.63	0.00
2.41	0.14				-0.20		0.02	-0.00		5	-116.30	242.94	9.65	0.00
13.83	0.17	0.02	-0.01	7.24	-0.26	1.02	-0.01	-0.00	-0.01	10	-110.86	243.00	9.70	0.00
2.23	0.15	0.01			-0.21		0.03	-0.00		6	-115.27	243.02	9.72	0.00
-1.02						0.42				2	-119.51	243.09	9.80	0.00
2.20	0.14			1.84	-0.19		-0.01			5	-116.42	243.18	9.88	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
1.97	0.15	0.01		3.13	-0.20		-0.01			6	-115.44	243.35	10.06	0.00
30.40			-0.03	1.66	-0.22			-0.00		5	-116.60	243.55	10.26	0.00
30.83			-0.03		-0.22		0.01	-0.00		5	-116.62	243.58	10.29	0.00
33.08		0.01	-0.03	2.95	-0.23			-0.00		6	-115.55	243.58	10.29	0.00
-1.34		0.01				0.45				3	-118.73	243.60	10.31	0.00
33.82		0.01	-0.03		-0.23		0.02	-0.00		6	-115.61	243.69	10.40	0.00
30.06			-0.03	1.82	-0.21		-0.02			5	-116.75	243.85	10.55	0.00
-34.90			0.03			0.48				3	-118.93	243.99	10.70	0.00
-1.66	0.12					0.42				3	-118.97	244.07	10.78	0.00
32.40		0.01	-0.03	3.08	-0.22		-0.02			6	-115.80	244.08	10.79	0.00
3.07				2.09	-0.19		0.02	-0.00		5	-116.91	244.16	10.87	0.00
2.93		0.01		3.36	-0.20		0.02	-0.00		6	-115.91	244.30	11.00	0.00
-36.12		0.01	0.03			0.51				4	-118.12	244.47	11.18	0.00
29.36	0.14	0.01	-0.03	2.62	-0.23			-0.00		7	-114.92	244.47	11.18	0.00
-2.02	0.13	0.01				0.44				4	-118.13	244.49	11.20	0.00
-0.50										1	-121.26	244.53	11.24	0.00
29.91	0.14	0.01	-0.03		-0.23		0.02	-0.00		7	-114.95	244.55	11.25	0.00
26.83	0.13		-0.02	1.32	-0.22			-0.00		6	-116.04	244.56	11.27	0.00
27.07	0.13		-0.02		-0.22		0.02	-0.00		6	-116.05	244.57	11.28	0.00
-38.99	0.14		0.04			0.49				4	-118.28	244.78	11.49	0.00
-1.05				4.32		0.44				3	-119.34	244.80	11.51	0.00
26.44	0.13		-0.02	1.46	-0.21		-0.01			6	-116.17	244.82	11.53	0.00
28.61	0.14	0.01	-0.03	2.74	-0.22		-0.02			7	-115.14	244.93	11.64	0.00
-0.91						0.42	-0.04			3	-119.41	244.95	11.66	0.00
2.22	0.15	0.01		2.97	-0.21		0.03	-0.00		7	-115.19	245.02	11.73	0.00
2.40	0.14			1.67	-0.19		0.02	-0.00		6	-116.28	245.03	11.74	0.00
-1.40		0.01		5.70		0.47				4	-118.44	245.10	11.81	0.00
-40.77	0.15	0.01	0.04			0.52				5	-117.39	245.13	11.83	0.00
-1.07						0.43		0.00		3	-119.50	245.13	11.84	0.00
-1.62		0.01				0.65			-0.00	4	-118.52	245.26	11.97	0.00
-0.74		0.00								2	-120.67	245.40	12.11	0.00
-1.16	0.13									2	-120.68	245.43	12.14	0.00
-1.22		0.01				0.45	-0.05			4	-118.60	245.43	12.14	0.00
-37.26			0.04	5.19		0.51				4	-118.68	245.59	12.29	0.00
30.23			-0.03	1.63	-0.22		0.01	-0.00		6	-116.60	245.67	12.38	0.00
-1.34		0.01				0.45		0.00		4	-118.73	245.69	12.40	0.00
32.87		0.01	-0.03	2.90	-0.23		0.02	-0.00		7	-115.54	245.71	12.42	0.00
-39.16		0.01	0.04	6.66		0.55				5	-117.73	245.80	12.51	0.00
-1.67	0.12			3.93		0.43				4	-118.82	245.87	12.58	0.00
-33.95			0.03			0.49	-0.04			4	-118.86	245.94	12.65	0.00
-1.55	0.12					0.42	-0.04			4	-118.87	245.96	12.67	0.00
-2.39	0.14	0.01				0.68			-0.00	5	-117.85	246.04	12.75	0.00
-35.16			0.03			0.49		0.00		4	-118.91	246.04	12.75	0.00
-2.07	0.13	0.01		5.32		0.47				5	-117.87	246.09	12.79	0.00
-1.73	0.12					0.43		0.00		4	-118.95	246.12	12.83	0.00
-1.45	0.13	0.01								3	-120.03	246.20	12.90	0.00
-17.32			0.02							2	-121.10	246.26	12.96	0.00
-33.89		0.01	0.03			0.66			-0.00	5	-118.01	246.35	13.06	0.00
-1.91	0.13	0.01				0.45	-0.05			5	-118.01	246.35	13.06	0.00
-35.02		0.01	0.03			0.52	-0.04			5	-118.03	246.40	13.11	0.00
-0.51				2.54						2	-121.19	246.45	13.16	0.00
-0.41							-0.03			2	-121.19	246.46	13.16	0.00
-41.14	0.13		0.04	4.83		0.51				5	-118.06	246.46	13.17	0.00
-0.44								-0.00		2	-121.23	246.53	13.23	0.00
-43.67	0.14	0.01	0.04	6.34		0.55				6	-117.04	246.55	13.26	0.00
-36.22		0.01	0.03			0.52		0.00		5	-118.12	246.58	13.29	0.00
-1.78		0.01		6.78		0.73			-0.00	5	-118.12	246.58	13.29	0.00
-2.04	0.13	0.01				0.45		0.00		5	-118.13	246.60	13.31	0.00
29.09	0.14	0.01	-0.03	2.57	-0.23		0.02	-0.00		8	-114.90	246.62	13.33	0.00
-0.94				4.41		0.44	-0.05			4	-119.23	246.67	13.38	0.00
26.62	0.13		-0.02	1.28	-0.22		0.02	-0.00		7	-116.03	246.71	13.41	0.00
-38.03	0.14		0.04			0.49	-0.03			5	-118.21	246.77	13.48	0.00
-39.34	0.14		0.04			0.50		0.00		5	-118.25	246.83	13.54	0.00
-1.01						0.45	-0.07	0.00		4	-119.31	246.85	13.55	0.00
-1.11				4.40		0.45		0.00		4	-119.32	246.86	13.57	0.00
-1.28		0.01		5.83		0.48	-0.05			5	-118.30	246.93	13.64	0.00
-38.38	0.15	0.01	0.04			0.70			-0.00	6	-117.23	246.93	13.64	0.00
-21.13	0.13		0.02							3	-120.46	247.05	13.76	0.00
-39.67	0.14	0.01	0.04			0.52	-0.04			6	-117.31	247.10	13.80	0.00
-17.31		0.00	0.02							3	-120.51	247.16	13.87	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
-1.42		0.01		5.72		0.47		0.00		5	-118.44	247.21	13.92	0.00
-1.50		0.01				0.64	-0.04		-0.00	5	-118.44	247.21	13.92	0.00
-0.77		0.01		3.58						3	-120.54	247.22	13.93	0.00
-40.94	0.15	0.01	0.04			0.52		0.00		6	-117.39	247.25	13.96	0.00
-0.65		0.00					-0.04			3	-120.60	247.33	14.03	0.00
-0.67		0.00						-0.00		3	-120.61	247.35	14.05	0.00
-1.66		0.01				0.66		0.00	-0.00	5	-118.51	247.37	14.07	0.00
-1.07	0.13						-0.03			3	-120.63	247.39	14.09	0.00
-1.15	0.12			2.15						3	-120.64	247.40	14.11	0.00
-1.28		0.01				0.47	-0.07	0.00		5	-118.55	247.45	14.15	0.00
-2.52	0.14	0.01		6.49		0.76			-0.01	6	-117.49	247.45	14.16	0.00
-1.11	0.13							-0.00		3	-120.66	247.46	14.17	0.00
-36.31			0.04	5.24		0.51	-0.04			5	-118.60	247.55	14.25	0.00
-36.46		0.01	0.03	7.42		0.75			-0.00	6	-117.54	247.55	14.26	0.00
-37.60			0.04	5.30		0.52		0.00		5	-118.65	247.64	14.35	0.00
-38.06		0.01	0.04	6.75		0.55	-0.04			6	-117.63	247.73	14.44	0.00
-1.56	0.12			4.01		0.44	-0.04			5	-118.72	247.78	14.48	0.00
-21.38	0.14	0.01	0.02							4	-119.81	247.85	14.56	0.00
-1.67	0.13					0.45	-0.07	0.00		5	-118.76	247.85	14.56	0.00
-33.94			0.03			0.51	-0.06	0.00		5	-118.76	247.86	14.57	0.00
-39.32		0.01	0.04	6.70		0.55		0.00		6	-117.73	247.93	14.63	0.00
-1.75	0.12			4.02		0.44		0.00		5	-118.79	247.93	14.64	0.00
-1.95	0.13	0.01		5.46		0.48	-0.05			6	-117.74	247.95	14.66	0.00
-2.27	0.14	0.01				0.67	-0.04		-0.00	6	-117.78	248.04	14.75	0.00
-1.46	0.13	0.01		3.22						4	-119.93	248.09	14.80	0.00
-1.35	0.13	0.01					-0.03			4	-119.97	248.16	14.87	0.00
-2.44	0.14	0.01				0.69		0.00	-0.00	6	-117.84	248.16	14.87	0.00
-18.10			0.02	2.82						3	-121.02	248.17	14.88	0.00
-1.37	0.13	0.01						-0.00		4	-119.98	248.19	14.90	0.00
-40.96	0.15	0.01	0.04	7.20		0.78			-0.00	7	-116.79	248.21	14.92	0.00
-2.10	0.13	0.01		5.35		0.47		0.00		6	-117.87	248.22	14.92	0.00
-16.49			0.02				-0.03			3	-121.05	248.23	14.94	0.00
-17.48			0.02					-0.00		3	-121.07	248.26	14.97	0.00
-33.22		0.01	0.03			0.65	-0.04		-0.00	6	-117.94	248.36	15.07	0.00
-1.99	0.13	0.01				0.47	-0.07	0.00		6	-117.95	248.37	15.08	0.00
-0.42				2.59			-0.03			3	-121.13	248.39	15.10	0.00
-35.05		0.01	0.03			0.54	-0.06	0.00		6	-117.98	248.44	15.14	0.00
-40.18	0.13		0.04	4.88		0.51	-0.04			6	-117.99	248.47	15.17	0.00
-0.45				2.49				-0.00		3	-121.17	248.47	15.18	0.00
-34.01		0.01	0.03			0.67		0.00	-0.00	6	-118.00	248.47	15.18	0.00
-0.40							-0.03	-0.00		3	-121.19	248.52	15.22	0.00
-41.59	0.13		0.04	4.96		0.53		0.00		6	-118.02	248.52	15.23	0.00
-42.56	0.14	0.01	0.04	6.43		0.56	-0.04			7	-116.94	248.53	15.24	0.00
-1.05				4.70		0.47	-0.07	0.00		5	-119.11	248.55	15.26	0.00
-1.65		0.01		6.79		0.72	-0.04		-0.00	6	-118.04	248.55	15.26	0.00
-38.07	0.14		0.04			0.52	-0.06	0.00		6	-118.10	248.68	15.39	0.00

Table B.2: Binomial regression model variations of *P. pantherinum* presence/absence against environmental parameters.

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
0.99		0.01			-0.18					3	-80.05	166.24	0.00	0.04
1.85		-0.00			-0.20	-0.46			0.01	5	-78.03	166.40	0.17	0.03
0.83		0.01		11.17	-0.18					4	-79.12	166.47	0.24	0.03
55.34		0.01	-0.05		-0.24					4	-79.26	166.75	0.51	0.03
0.73		0.02		12.87	-0.21	0.39				5	-78.28	166.90	0.66	0.03
1.63		0.00		10.33	-0.20	-0.32			0.01	6	-77.26	166.99	0.75	0.02
0.94		0.01			-0.21	0.33				4	-79.43	167.08	0.84	0.02
51.55		0.02	-0.05	10.58	-0.23					5	-78.45	167.25	1.01	0.02
1.40		0.01			-0.19			-0.00		4	-79.66	167.55	1.31	0.02
2.34		-0.00			-0.21	-0.56		-0.00	0.01	6	-77.63	167.74	1.51	0.02
1.27		0.02		11.10	-0.19			-0.00		5	-78.71	167.75	1.52	0.02
38.70		-0.00	-0.04		-0.24	-0.48			0.01	6	-77.72	167.92	1.68	0.02
57.48		0.02	-0.06		-0.25			-0.00		5	-78.84	168.02	1.78	0.01
0.89		0.01			-0.19		0.06			4	-79.94	168.10	1.87	0.01
46.26		0.01	-0.04		-0.25	0.25				5	-78.92	168.18	1.95	0.01
0.85	0.03	0.01			-0.19					4	-80.03	168.29	2.05	0.01
39.35		0.02	-0.04	12.09	-0.24	0.32				6	-77.93	168.33	2.09	0.01
2.12		0.00		9.91	-0.21	-0.42		-0.00	0.01	7	-76.88	168.41	2.17	0.01
0.74		0.01		11.11	-0.18		0.05			5	-79.06	168.46	2.22	0.01
53.92		0.02	-0.05	10.49	-0.25			-0.00		6	-78.00	168.48	2.24	0.01
1.08		0.02		12.69	-0.21	0.35		-0.00		6	-78.02	168.52	2.28	0.01
1.82		-0.00			-0.20	-0.45	0.02		0.01	6	-78.03	168.53	2.29	0.01
1.88	-0.01	-0.00			-0.20	-0.46			0.01	6	-78.03	168.54	2.30	0.01
0.72	0.02	0.01		11.11	-0.18					5	-79.11	168.56	2.33	0.01
1.46		0.01			-0.21		0.15	-0.00		5	-79.12	168.58	2.34	0.01
1.26		0.01			-0.21	0.29		-0.00		5	-79.18	168.70	2.47	0.01
54.46		0.01	-0.05		-0.24		0.05			5	-79.18	168.70	2.47	0.01
33.11		0.00	-0.03	9.80	-0.23	-0.35			0.01	7	-77.03	168.71	2.47	0.01
54.98	0.01	0.01	-0.05		-0.24					5	-79.26	168.86	2.62	0.01
-2.25		0.01								2	-82.40	168.87	2.63	0.01
-2.36		0.01		11.10						3	-81.41	168.94	2.71	0.01
0.68		0.02		12.80	-0.21	0.38	0.03			6	-78.25	168.97	2.74	0.01
1.30		0.02		10.87	-0.21		0.14	-0.00		6	-78.27	169.01	2.77	0.01
0.65	0.02	0.02		12.82	-0.21	0.39				6	-78.27	169.02	2.78	0.01
0.87		0.01			-0.21	0.32	0.05			5	-79.35	169.03	2.79	0.01
57.47		0.02	-0.06		-0.27		0.15	-0.00		6	-78.33	169.14	2.90	0.01
1.68	-0.01	0.00		10.34	-0.20	-0.33			0.01	7	-77.25	169.15	2.91	0.01
1.62		0.00		10.33	-0.20	-0.32	0.00		0.01	7	-77.26	169.15	2.91	0.01
0.81	0.03	0.01			-0.21	0.33				5	-79.41	169.16	2.93	0.01
40.96		-0.00	-0.04		-0.24	-0.58		-0.00	0.01	7	-77.30	169.24	3.00	0.01
50.87		0.02	-0.05	10.53	-0.23		0.04			6	-78.41	169.30	3.06	0.01
51.37	0.01	0.02	-0.05	10.56	-0.23					6	-78.45	169.38	3.15	0.01
2.35		-0.00			-0.22	-0.55	0.10	-0.00	0.01	7	-77.42	169.47	3.24	0.01
-1.43		-0.00				-0.67			0.01	4	-80.65	169.53	3.29	0.01
1.28	0.02	0.01			-0.19			-0.00		5	-79.65	169.64	3.40	0.01
1.45					-0.17					2	-82.81	169.69	3.45	0.01
49.73		0.02	-0.05		-0.25	0.21		-0.00		6	-78.61	169.71	3.47	0.01
53.78		0.02	-0.05	10.26	-0.26		0.13	-0.00		7	-77.59	169.82	3.58	0.01
43.00		0.02	-0.04	11.83	-0.25	0.28		-0.00		7	-77.61	169.87	3.63	0.01
1.20	0.02	0.02		11.06	-0.19			-0.00		6	-78.70	169.88	3.65	0.01
2.43	-0.02	-0.00			-0.21	-0.57		-0.00	0.01	7	-77.63	169.89	3.66	0.01
1.35		0.02			-0.22	0.25	0.13	-0.00		6	-78.78	170.03	3.79	0.01
38.64		-0.00	-0.04		-0.24	-0.48	0.01		0.01	7	-77.71	170.07	3.83	0.01
39.05	-0.01	-0.00	-0.04		-0.24	-0.49			0.01	7	-77.72	170.07	3.84	0.01
35.68		0.00	-0.03	9.36	-0.24	-0.44		-0.00	0.01	8	-76.64	170.11	3.87	0.01
1.14		0.02		12.30	-0.22	0.32	0.11	-0.00		7	-77.74	170.13	3.89	0.01
57.41	0.00	0.02	-0.06		-0.25			-0.00		6	-78.84	170.16	3.92	0.01
0.72	0.03	0.01			-0.19		0.06			5	-79.91	170.16	3.93	0.00
45.65		0.01	-0.04		-0.25	0.25	0.05			6	-78.85	170.19	3.95	0.00
-1.69		-0.00		9.40		-0.53			0.01	5	-79.94	170.22	3.98	0.00
2.12		0.00		9.71	-0.22	-0.41	0.09	-0.00	0.01	8	-76.73	170.28	4.04	0.00
45.88	0.01	0.01	-0.04		-0.25	0.25				6	-78.92	170.31	4.08	0.00
-2.69		0.01		12.19		0.25				4	-81.05	170.33	4.09	0.00
39.01		0.02	-0.04	12.02	-0.24	0.32	0.03			7	-77.90	170.44	4.20	0.00
39.17	0.01	0.02	-0.04	12.07	-0.24	0.32				7	-77.92	170.49	4.25	0.00
-2.06		0.01						-0.00		3	-82.20	170.53	4.29	0.00
-2.48		0.01				0.18				3	-82.20	170.53	4.29	0.00
0.61	0.03	0.02		11.04	-0.18		0.05			6	-79.04	170.57	4.33	0.00
2.23	-0.02	0.00		9.93	-0.21	-0.43		-0.00	0.01	8	-76.88	170.58	4.34	0.00
-2.18		0.01		11.05				-0.00		4	-81.21	170.64	4.40	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
54.10	-0.00	0.02	-0.05	10.51	-0.25			-0.00		7	-78.00	170.64	4.40	0.00
1.02	0.01	0.02		12.65	-0.21	0.35		-0.00		7	-78.02	170.68	4.44	0.00
1.32	0.03	0.01			-0.21		0.16	-0.00		6	-79.10	170.68	4.44	0.00
1.84	-0.00	-0.00			-0.20	-0.45	0.02		0.01	7	-78.02	170.69	4.45	0.00
44.69			-0.04		-0.21					3	-82.28	170.70	4.46	0.00
1.39				7.78	-0.17					3	-82.30	170.73	4.49	0.00
1.16	0.02	0.01			-0.21	0.29		-0.00		6	-79.17	170.82	4.58	0.00
53.95	0.01	0.01	-0.05		-0.24		0.05			6	-79.18	170.83	4.59	0.00
-2.33		0.01					0.03			3	-82.37	170.87	4.64	0.00
33.53	-0.02	0.00	-0.03	9.82	-0.23	-0.35			0.01	8	-77.03	170.89	4.65	0.00
1.42					-0.19	0.27				3	-82.38	170.89	4.65	0.00
33.09		0.00	-0.03	9.80	-0.23	-0.35	0.00		0.01	8	-77.03	170.90	4.66	0.00
-2.34	0.02	0.01								3	-82.39	170.92	4.69	0.00
1.86		0.01	-0.00							3	-82.40	170.93	4.69	0.00
42.33		0.00	-0.04		-0.25	-0.57	0.10	-0.00	0.01	8	-77.07	170.96	4.73	0.00
-2.43		0.01		11.07			0.03			4	-81.38	170.99	4.75	0.00
51.29		0.02	-0.05		-0.27	0.17	0.14	-0.00		7	-78.19	171.03	4.79	0.00
-2.41	0.01	0.01		11.08						4	-81.40	171.03	4.80	0.00
-1.30		0.01	-0.00	11.09						4	-81.40	171.03	4.80	0.00
-1.11		-0.00				-0.75		-0.00	0.01	5	-80.38	171.10	4.86	0.00
0.58	0.02	0.02		12.73	-0.21	0.38	0.03			7	-78.24	171.12	4.88	0.00
0.72	0.03	0.01			-0.21	0.32	0.05			6	-79.33	171.13	4.89	0.00
1.20	0.02	0.02		10.81	-0.21		0.14	-0.00		7	-78.26	171.15	4.92	0.00
57.22	0.01	0.02	-0.05		-0.27		0.15	-0.00		7	-78.33	171.30	5.06	0.00
1.67	-0.01	0.00		10.34	-0.20	-0.32	0.00		0.01	8	-77.25	171.34	5.10	0.00
1.75					-0.17			-0.00		3	-82.62	171.38	5.14	0.00
41.66	-0.03	-0.00	-0.04		-0.24	-0.59		-0.00	0.01	8	-77.29	171.40	5.16	0.00
50.58	0.01	0.02	-0.05	10.51	-0.23		0.04			7	-78.41	171.46	5.22	0.00
44.49		0.02	-0.04	11.41	-0.26	0.24	0.12	-0.00		8	-77.32	171.47	5.23	0.00
-13.48		-0.00	0.01			-0.66			0.01	5	-80.61	171.56	5.32	0.00
1.35					-0.17		0.05			3	-82.72	171.57	5.33	0.00
-1.39		-0.00				-0.68	-0.01		0.01	5	-80.65	171.63	5.40	0.00
-1.37	-0.01	-0.00				-0.68			0.01	5	-80.65	171.64	5.40	0.00
2.41	-0.01	-0.00			-0.22	-0.56	0.10	-0.00	0.01	8	-77.41	171.66	5.42	0.00
-1.55										1	-84.82	171.67	5.43	0.00
1.34				9.06	-0.19	0.32				4	-81.72	171.67	5.43	0.00
1.40	0.01				-0.17					3	-82.81	171.75	5.51	0.00
49.61	0.00	0.02	-0.05		-0.25	0.21		-0.00		7	-78.61	171.87	5.63	0.00
-1.40		-0.00		9.04		-0.60		-0.00	0.01	6	-79.73	171.93	5.69	0.00
41.19			-0.04	7.13	-0.21					4	-81.86	171.95	5.71	0.00
37.00		0.00	-0.03	9.14	-0.25	-0.44	0.09	-0.00	0.01	9	-76.47	171.97	5.74	0.00
53.77	0.00	0.02	-0.05	10.26	-0.26		0.13	-0.00		8	-77.59	172.01	5.77	0.00
43.13	-0.00	0.02	-0.04	11.83	-0.25	0.28		-0.00		8	-77.61	172.05	5.82	0.00
1.23	0.03	0.02			-0.22	0.25	0.14	-0.00		7	-78.76	172.17	5.93	0.00
-2.51		0.01		12.05		0.22		-0.00		5	-80.92	172.19	5.95	0.00
-19.16		-0.00	0.02	9.76		-0.50			0.01	6	-79.86	172.19	5.95	0.00
38.96	-0.01	-0.00	-0.04		-0.24	-0.48	0.01		0.01	8	-77.71	172.25	6.01	0.00
-2.20		0.01					0.08	-0.00		4	-82.01	172.25	6.01	0.00
38.40			-0.04		-0.22	0.22				4	-82.02	172.26	6.02	0.00
36.47	-0.03	0.00	-0.03	9.39	-0.24	-0.45		-0.00	0.01	9	-76.62	172.29	6.05	0.00
1.07	0.02	0.02		12.25	-0.22	0.31	0.11	-0.00		8	-77.74	172.30	6.07	0.00
-2.29		0.01				0.16		-0.00		4	-82.05	172.32	6.09	0.00
45.15	0.01	0.01	-0.04		-0.25	0.25	0.05			7	-78.85	172.34	6.10	0.00
-1.60	-0.02	-0.00		9.44		-0.53			0.01	6	-79.93	172.35	6.11	0.00
-1.65		-0.00		9.41		-0.53	-0.01		0.01	6	-79.94	172.35	6.11	0.00
-12.49		0.01	0.01	12.42		0.27				5	-81.02	172.38	6.15	0.00
45.60			-0.04		-0.22			-0.00		4	-82.09	172.40	6.16	0.00
-2.72		0.01		12.15		0.24	0.01			5	-81.05	172.43	6.19	0.00
-2.31		0.01		10.91			0.08	-0.00		5	-81.05	172.43	6.20	0.00
-2.70	0.00	0.01		12.18		0.25				5	-81.05	172.44	6.20	0.00
1.70				7.62	-0.17			-0.00		4	-82.12	172.46	6.22	0.00
2.20	-0.01	0.00		9.73	-0.22	-0.42	0.09	-0.00	0.01	9	-76.72	172.48	6.25	0.00
-2.54		0.01				0.18	0.02			4	-82.18	172.59	6.35	0.00
-1.58				7.88						2	-84.27	172.60	6.36	0.00
1.91		0.01	-0.00					-0.00		4	-82.19	172.61	6.37	0.00
-2.13	0.01	0.01						-0.00		4	-82.19	172.61	6.37	0.00
-2.55	0.01	0.01				0.18				4	-82.19	172.61	6.38	0.00
-5.78		0.01	0.00			0.19				4	-82.19	172.61	6.38	0.00
38.75	0.01	0.02	-0.04	12.00	-0.24	0.32	0.03			8	-77.90	172.63	6.39	0.00
43.82			-0.04		-0.21		0.05			4	-82.22	172.66	6.42	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
1.30				7.71	-0.17		0.04			4	-82.23	172.69	6.45	0.00
1.79					-0.19		0.12	-0.00		4	-82.26	172.75	6.51	0.00
-1.38		0.01	-0.00	11.04				-0.00		5	-81.21	172.75	6.52	0.00
-2.20	0.00	0.01		11.04				-0.00		5	-81.21	172.75	6.52	0.00
44.80	-0.00		-0.04		-0.21					4	-82.28	172.79	6.55	0.00
1.64					-0.19	0.24		-0.00		4	-82.29	172.80	6.56	0.00
1.34					-0.19	0.27	0.05			4	-82.29	172.81	6.57	0.00
1.38	0.00			7.77	-0.17					4	-82.30	172.82	6.58	0.00
-2.44	0.02	0.01					0.03			4	-82.36	172.95	6.71	0.00
0.84		0.01	-0.00				0.03			4	-82.37	172.96	6.72	0.00
1.38	0.01				-0.19	0.27				4	-82.38	172.98	6.74	0.00
1.29	0.02	0.01	-0.00							4	-82.39	173.01	6.77	0.00
33.52	-0.02	0.00	-0.03	9.82	-0.23	-0.35	0.00		0.01	9	-77.03	173.10	6.86	0.00
-2.49	0.01	0.01		11.04			0.03			5	-81.38	173.10	6.86	0.00
-2.13		0.01	-0.00	11.07			0.03			5	-81.38	173.11	6.87	0.00
-1.59	0.01	0.01	-0.00	11.07						5	-81.40	173.15	6.91	0.00
-13.36		-0.00	0.01			-0.74		-0.00	0.01	6	-80.34	173.15	6.92	0.00
-1.17		-0.00				-0.76	0.04	-0.00	0.01	6	-80.34	173.16	6.92	0.00
42.93	-0.02	0.00	-0.04		-0.25	-0.58	0.10	-0.00	0.01	9	-77.06	173.16	6.92	0.00
51.03	0.01	0.02	-0.05		-0.27	0.17	0.14	-0.00		8	-78.19	173.21	6.98	0.00
-1.00	-0.02	-0.00				-0.76		-0.00	0.01	6	-80.37	173.22	6.98	0.00
32.91			-0.03	8.35	-0.21	0.27				5	-81.47	173.27	7.03	0.00
1.72	0.01				-0.17			-0.00		4	-82.62	173.47	7.23	0.00
-1.72						0.14				2	-84.71	173.48	7.24	0.00
-1.43								-0.00		2	-84.75	173.56	7.33	0.00
1.55				8.86	-0.19	0.29		-0.00		5	-81.64	173.63	7.39	0.00
-1.64							0.03			2	-84.79	173.64	7.41	0.00
1.30	0.01				-0.17		0.05			4	-82.72	173.66	7.42	0.00
1.26				8.99	-0.19	0.32	0.04			5	-81.67	173.67	7.44	0.00
44.49	0.00	0.02	-0.04	11.41	-0.26	0.24	0.12	-0.00		9	-77.32	173.68	7.44	0.00
42.12			-0.04	6.97	-0.21			-0.00		5	-81.67	173.68	7.44	0.00
-13.29		-0.00	0.01			-0.66	-0.01		0.01	6	-80.61	173.69	7.45	0.00
-13.29	-0.01	-0.00	0.01			-0.66			0.01	6	-80.61	173.70	7.46	0.00
-0.25			-0.00							2	-84.82	173.71	7.47	0.00
-1.56	0.00									2	-84.82	173.71	7.48	0.00
-1.32	-0.01	-0.00				-0.68	-0.01		0.01	6	-80.64	173.77	7.53	0.00
1.34	0.00			9.05	-0.19	0.32				5	-81.72	173.79	7.55	0.00
44.83			-0.04		-0.23		0.12	-0.00		5	-81.76	173.87	7.63	0.00
-18.91		-0.00	0.02	9.39		-0.58		-0.00	0.01	7	-79.64	173.92	7.69	0.00
40.49			-0.04	7.09	-0.21		0.04			5	-81.81	173.97	7.73	0.00
1.73				7.35	-0.18		0.11	-0.00		5	-81.82	173.97	7.73	0.00
-1.45		-0.00		8.95		-0.61	0.04	-0.00	0.01	7	-79.70	174.03	7.80	0.00
41.46	-0.01		-0.04	7.16	-0.21					5	-81.86	174.06	7.82	0.00
-1.25	-0.03	-0.00		9.10		-0.61		-0.00	0.01	7	-79.71	174.06	7.82	0.00
40.09			-0.04		-0.22	0.19		-0.00		5	-81.90	174.14	7.90	0.00
-2.57		0.01		11.82		0.20	0.06	-0.00		6	-80.84	174.16	7.92	0.00
-2.36		0.01				0.13	0.07	-0.00		5	-81.92	174.18	7.95	0.00
37.70	-0.02	0.00	-0.03	9.17	-0.25	-0.45	0.09	-0.00	0.01	10	-76.45	174.19	7.95	0.00
37.53			-0.04		-0.22	0.22	0.05			5	-81.95	174.23	8.00	0.00
-1.81				8.64		0.18				3	-84.06	174.26	8.02	0.00
-11.43		0.01	0.01	12.26		0.24		-0.00		6	-80.90	174.28	8.04	0.00
-2.50	-0.00	0.01		12.06		0.22		-0.00		6	-80.92	174.33	8.09	0.00
-18.96		-0.00	0.02	9.77		-0.51	-0.01		0.01	7	-79.85	174.35	8.11	0.00
1.70					-0.20	0.22	0.11	-0.00		5	-82.00	174.35	8.11	0.00
-18.81	-0.01	-0.00	0.02	9.78		-0.51			0.01	7	-79.85	174.35	8.11	0.00
-2.27	0.01	0.01					0.09	-0.00		5	-82.01	174.36	8.12	0.00
-0.61		0.01	-0.00				0.08	-0.00		5	-82.01	174.36	8.13	0.00
38.44	-0.00		-0.04		-0.22	0.22				5	-82.02	174.37	8.13	0.00
-2.34	0.01	0.01				0.16		-0.00		5	-82.05	174.43	8.20	0.00
-4.55		0.01	0.00			0.16		-0.00		5	-82.05	174.43	8.20	0.00
-1.54	-0.02	-0.00		9.45		-0.54	-0.02		0.01	7	-79.93	174.49	8.26	0.00
-12.86		0.01	0.01	12.39		0.26	0.02			6	-81.02	174.51	8.27	0.00
45.81	-0.01		-0.04		-0.22			-0.00		5	-82.09	174.51	8.27	0.00
-12.71	0.01	0.01	0.01	12.41		0.27				6	-81.02	174.52	8.28	0.00
-1.47				7.79				-0.00		3	-84.20	174.54	8.30	0.00
-2.73	0.00	0.01		12.14		0.24	0.01			6	-81.04	174.57	8.33	0.00
1.71	-0.00			7.63	-0.17			-0.00		5	-82.12	174.57	8.33	0.00
-3.75		0.01	0.00	10.93			0.08	-0.00		6	-81.05	174.57	8.33	0.00
-2.33	0.00	0.01		10.90			0.08	-0.00		6	-81.05	174.57	8.34	0.00
-1.66				7.85			0.03			3	-84.24	174.61	8.37	0.00

(Int)	Depth	Lunar	Pressure	Rain	SST	Tide	Wind Ave	Wind Dir	Lunar*Tide	df	LogLik	AICc	delta	weight
-1.54	-0.01			7.91						3	-84.26	174.66	8.43	0.00
-3.25			0.00	7.91						3	-84.26	174.66	8.43	0.00
-2.61	0.01	0.01				0.18	0.02			5	-82.18	174.69	8.46	0.00
-6.39		0.01	0.00			0.18	0.02			5	-82.18	174.69	8.46	0.00
1.52	0.01	0.01	-0.00					-0.00		5	-82.19	174.72	8.48	0.00
-6.30	0.01	0.01	0.00			0.19				5	-82.19	174.72	8.48	0.00
43.89	-0.00		-0.04		-0.21		0.05			5	-82.22	174.77	8.53	0.00
1.28	0.00			7.70	-0.17		0.04			5	-82.23	174.81	8.57	0.00
1.75	0.01				-0.19		0.12	-0.00		5	-82.26	174.86	8.62	0.00
-1.45	0.00	0.01	-0.00	11.03				-0.00		6	-81.21	174.89	8.65	0.00
1.60	0.01				-0.19	0.24		-0.00		5	-82.28	174.91	8.67	0.00
1.29	0.01				-0.19	0.27	0.05			5	-82.29	174.92	8.68	0.00
0.17	0.02	0.01	-0.00				0.03			5	-82.36	175.06	8.82	0.00
34.56			-0.03	8.10	-0.22	0.24		-0.00		6	-81.37	175.21	8.97	0.00
-13.94		-0.00	0.01			-0.74	0.04	-0.00	0.01	7	-80.29	175.23	8.99	0.00
-2.51	0.01	0.01	0.00	11.04			0.03			6	-81.38	175.24	9.00	0.00
41.48			-0.04	6.71	-0.22		0.11	-0.00		6	-81.40	175.27	9.03	0.00
-12.94	-0.02	-0.00	0.01			-0.74		-0.00	0.01	7	-80.33	175.30	9.07	0.00
-1.06	-0.02	-0.00				-0.76	0.04	-0.00	0.01	7	-80.33	175.30	9.07	0.00
32.28			-0.03	8.31	-0.21	0.27	0.04			6	-81.42	175.32	9.08	0.00
1.59				8.51	-0.20	0.27	0.09	-0.00		6	-81.44	175.35	9.11	0.00
-1.53							0.07	-0.00		3	-84.62	175.38	9.14	0.00
33.12	-0.01		-0.03	8.38	-0.21	0.27				6	-81.46	175.41	9.17	0.00
-1.60						0.12		-0.00		3	-84.66	175.46	9.22	0.00
-1.79						0.13	0.03			3	-84.68	175.49	9.26	0.00
-5.19			0.00			0.14				3	-84.70	175.54	9.30	0.00
-1.73	0.00					0.14				3	-84.71	175.55	9.31	0.00
-0.44			-0.00					-0.00		3	-84.75	175.63	9.39	0.00
-1.43	0.00							-0.00		3	-84.75	175.63	9.39	0.00
-1.66	0.00						0.03			3	-84.79	175.71	9.47	0.00
-1.21			-0.00				0.03			3	-84.79	175.71	9.47	0.00
40.16			-0.04		-0.23	0.16	0.11	-0.00		6	-81.62	175.73	9.49	0.00
1.55	-0.00			8.86	-0.19	0.29		-0.00		6	-81.64	175.77	9.53	0.00
-0.31	0.00		-0.00							3	-84.82	175.78	9.54	0.00
42.51	-0.01		-0.04	7.01	-0.21			-0.00		6	-81.67	175.81	9.57	0.00
1.25	0.00			8.98	-0.19	0.32	0.04			6	-81.67	175.81	9.57	0.00
-13.06	-0.01	-0.00	0.01			-0.66	-0.01		0.01	7	-80.61	175.85	9.61	0.00
45.00	-0.01		-0.04		-0.23		0.11	-0.00		6	-81.76	176.00	9.77	0.00
-19.36		-0.00	0.02	9.30		-0.58	0.04	-0.00	0.01	8	-79.61	176.05	9.81	0.00
-18.33	-0.02	-0.00	0.02	9.43		-0.59		-0.00	0.01	8	-79.63	176.09	9.85	0.00
40.73	-0.01		-0.04	7.11	-0.21		0.04			6	-81.81	176.10	9.86	0.00
1.72	0.00			7.35	-0.18		0.11	-0.00		6	-81.82	176.11	9.87	0.00
-1.31	-0.02	-0.00		9.00		-0.61	0.03	-0.00	0.01	8	-79.68	176.19	9.96	0.00
-12.22		0.01	0.01	12.04		0.22	0.06	-0.00		7	-80.81	176.27	10.03	0.00
40.23	-0.00		-0.04		-0.22	0.19		-0.00		6	-81.90	176.27	10.04	0.00
-1.72				8.52		0.17		-0.00		4	-84.04	176.30	10.06	0.00

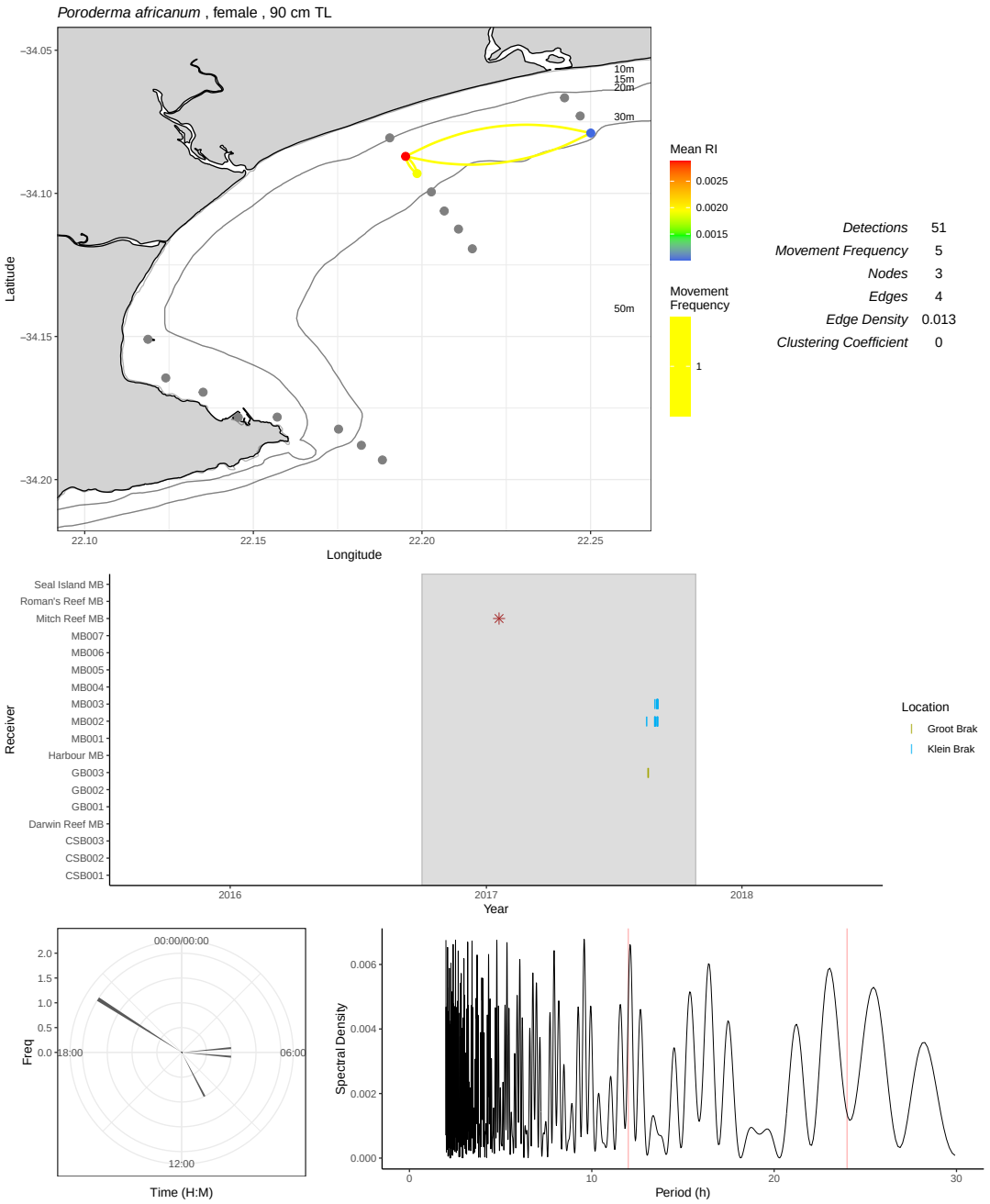
Appendix C
Movement Behaviour Summary of Acoustically Tagged *Poroderma* Individuals

The following pages show a summary of the movement behaviour of each detected tagged *Poroderma* individual (excluding ID 23633 due to lack of detections). Each summary is composed of the following elements:

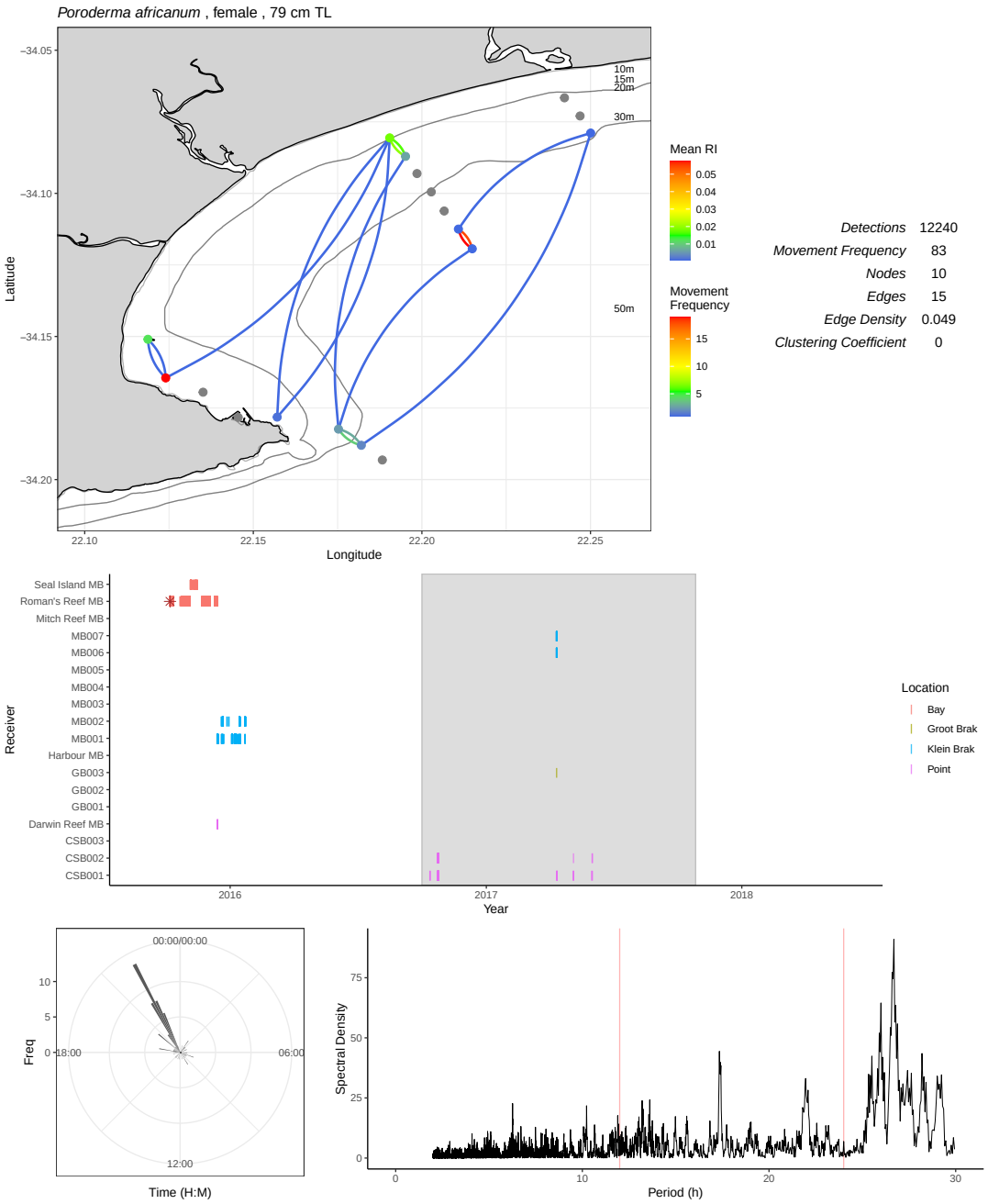
- The tag ID.
- Species, sex and size of the individual.
- A network graph of the movement across the Mossel Bay receiver network. Each graph was coloured according to the RI at each receiver and frequency of movement between receivers. Each graph is accompanied by a summary of the number of detections, total number of movements between receivers, the number of receivers it was detected on, number of edges, edge density and clustering coefficient.
- An abacus plot of detections of the individual per receiver, coloured according the CRT grouping (Figure 5.1). The grey square indicates the period (October 2016 until October 2017) during which three receivers were lost.
- A circular plot showing departure times from receivers (over a 24h period).
- Spectral plots using FFT of each tagged individual. Each plot was marked with a red line on the 12.5 and 24 hour marks.

The methodology of each item is described in Chapter 5.

ID: 23633b

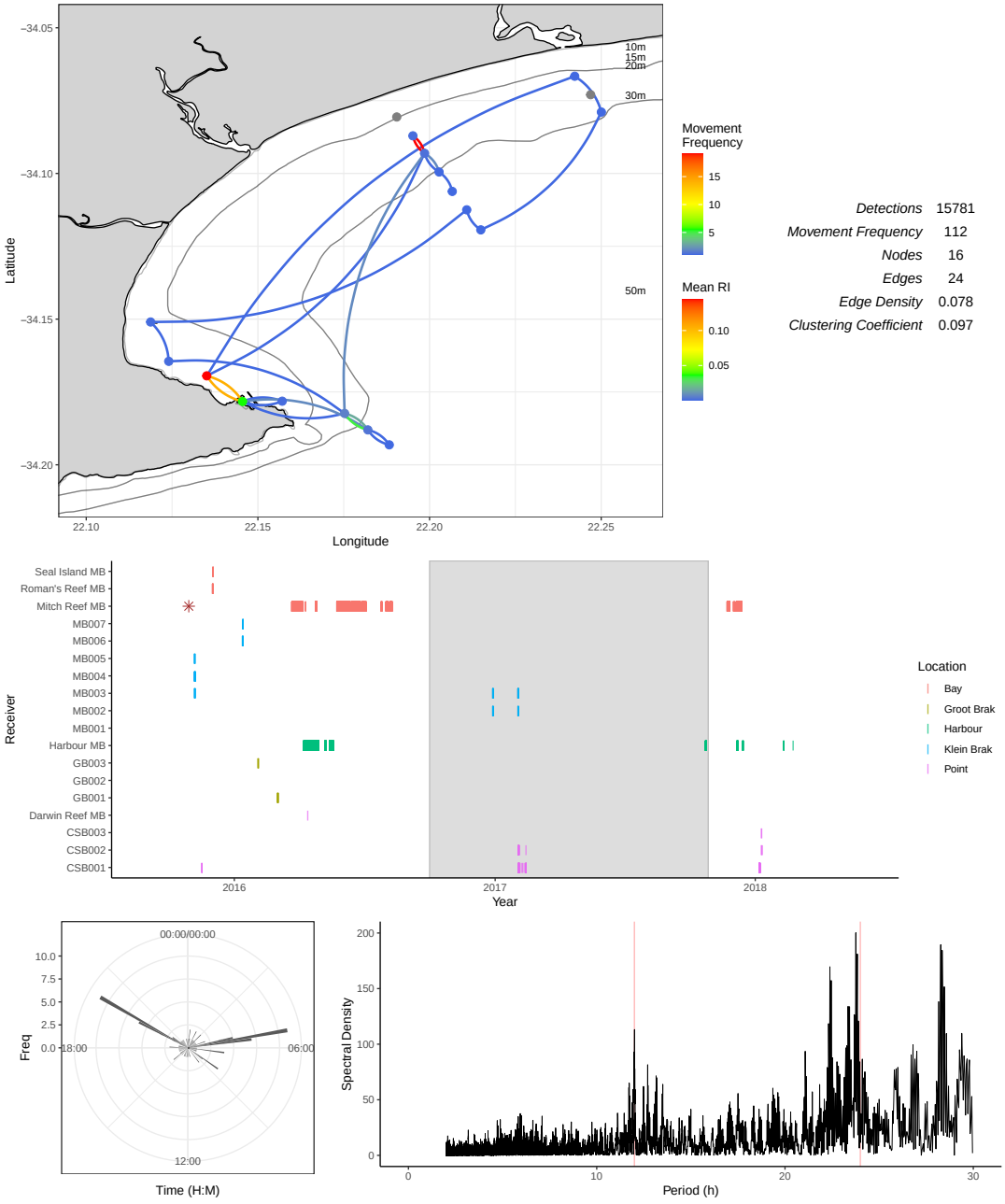

Poroderma africanum , female , 90 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
0.0025
0.0020
0.0015
Movement Frequency
1
Detections 51
Movement Frequency 5
Nodes 3
Edges 4
Edge Density 0.013
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Groot Brak
Klein Brak
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25862

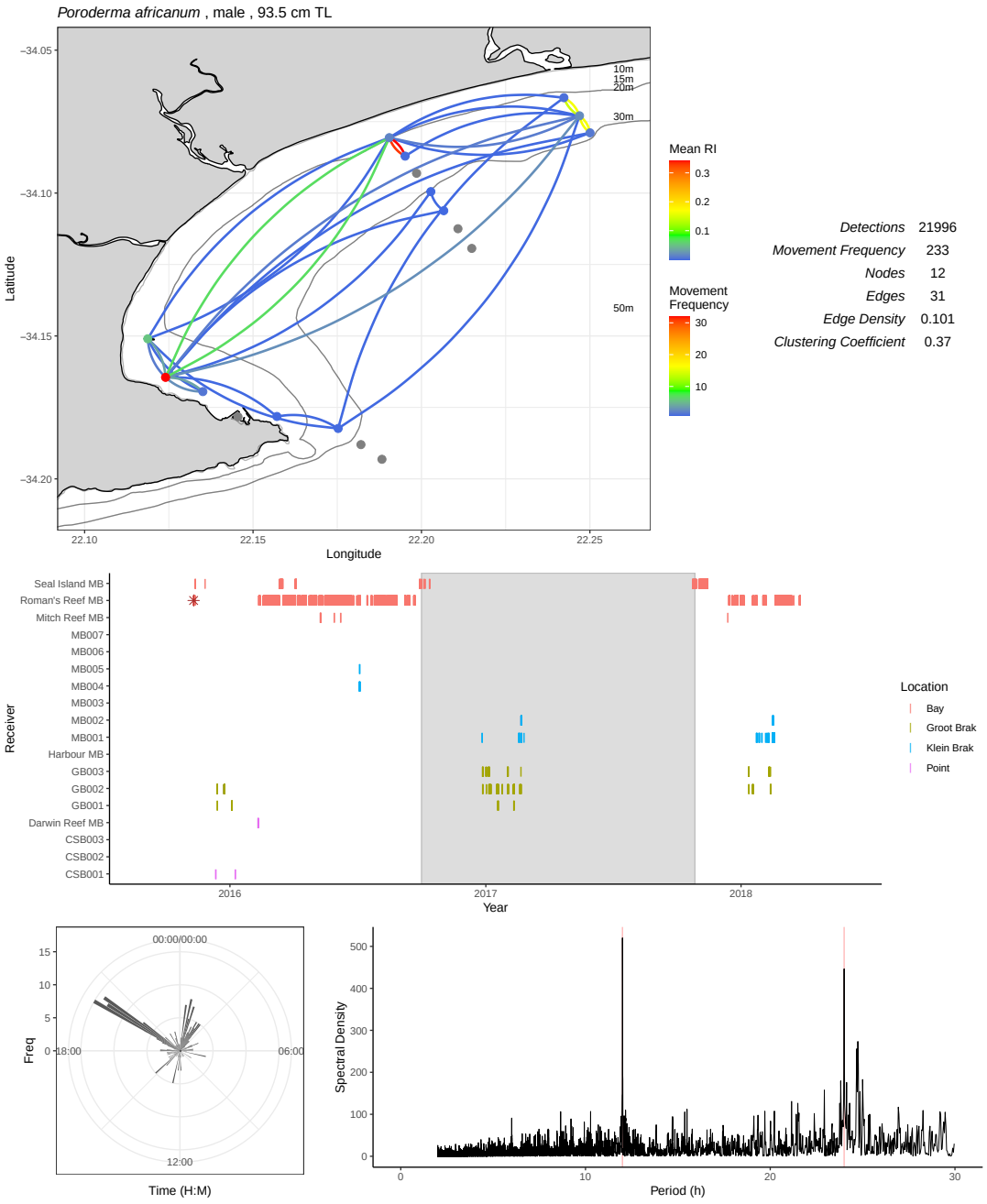

Poroderma africanum , female , 79 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 12240
Movement Frequency 83
Nodes 10
Edges 15
Edge Density 0.049
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Bay
Groot Brak
Klein Brak
Point
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25863

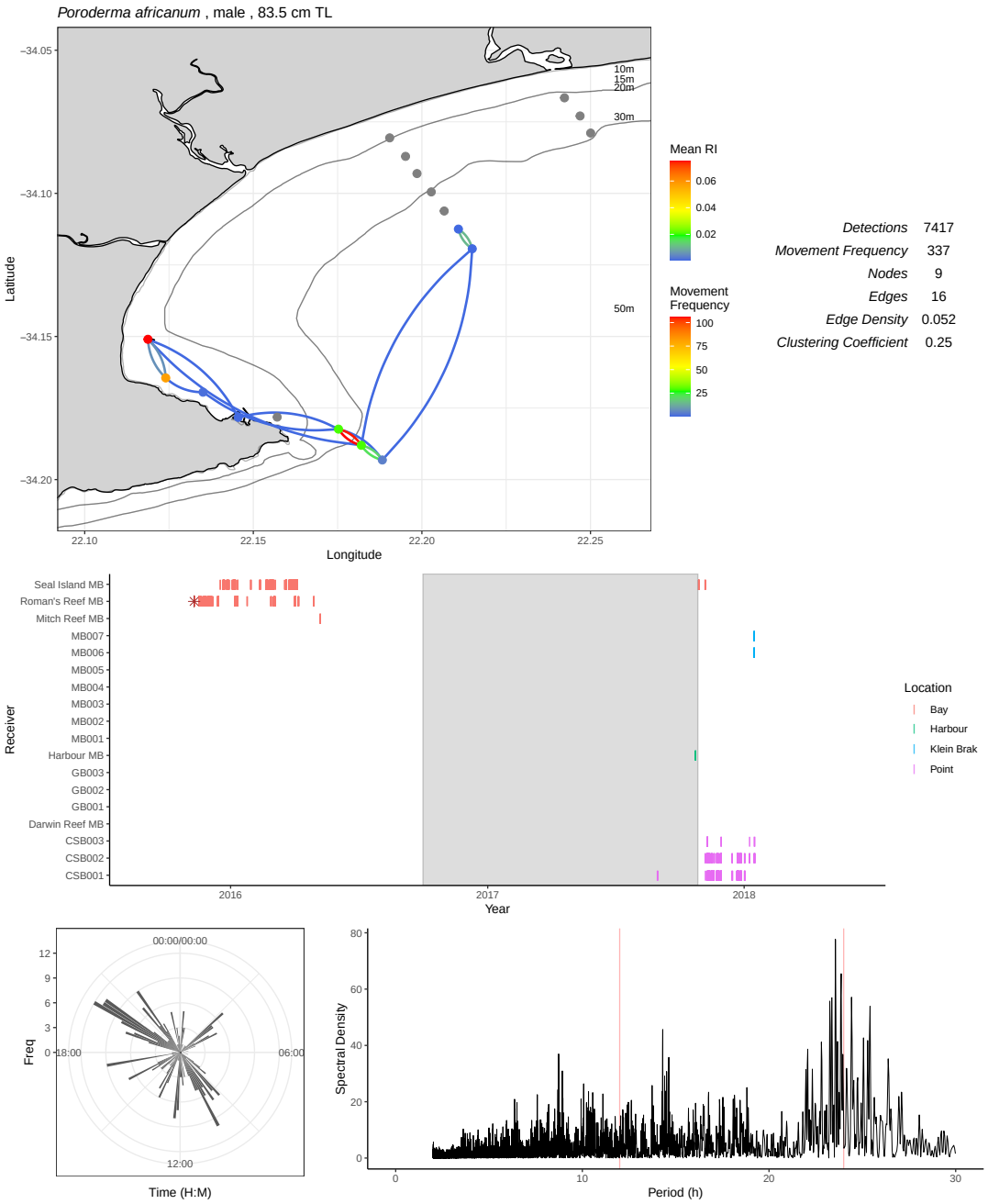
Poroderma africanum , male , 84.5 cm TL



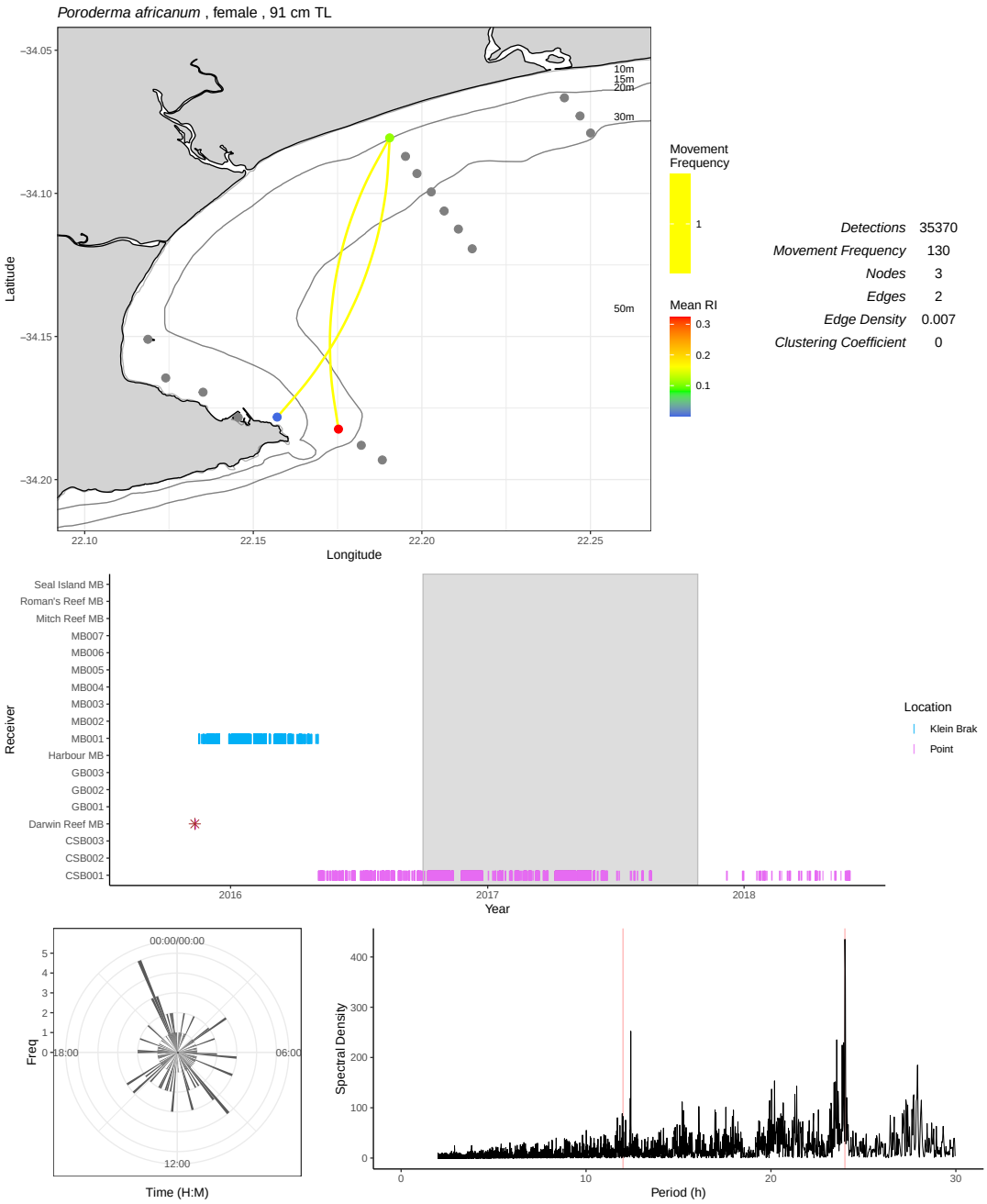
ID: 25864


Poroderma africanum , male , 93.5 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 21996
Movement Frequency 233
Nodes 12
Edges 31
Edge Density 0.101
Clustering Coefficient 0.37
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
Harbour MB
Darwin Reef MB
Year
Location
Bay
Groot Brak
Klein Brak
Point
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25865

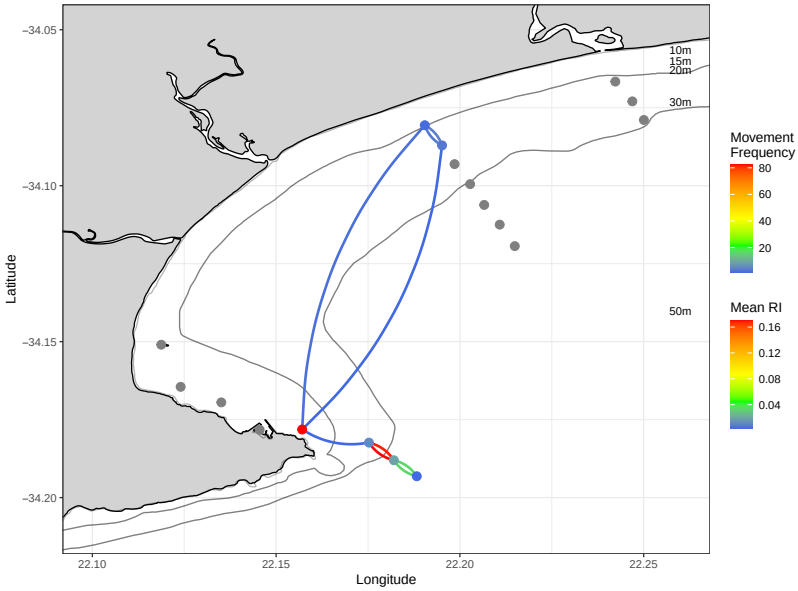

Poroderma africanum , male , 83.5 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 7417
Movement Frequency 337
Nodes 9
Edges 16
Edge Density 0.052
Clustering Coefficient 0.25
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
Harbour MB
Darwin Reef MB
Year
Location
Bay
Harbour
Klein Brak
Point
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25866

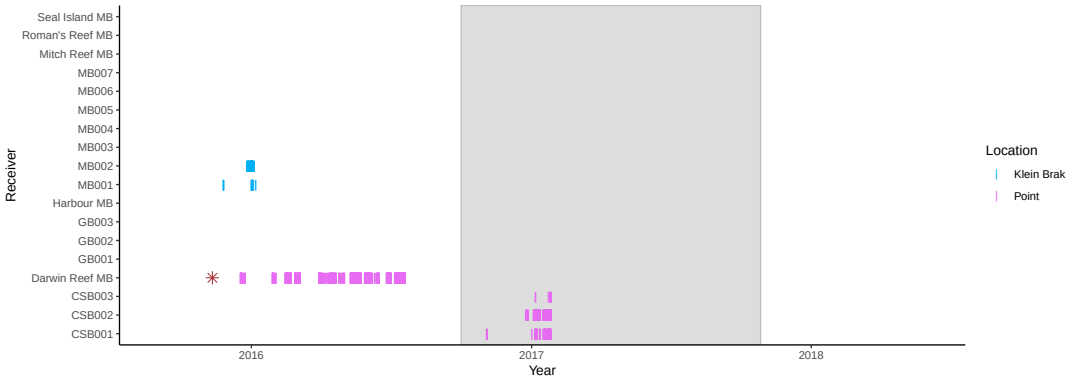

Poroderma africanum , female , 91 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Movement Frequency
Mean RI
Detections 35370
Movement Frequency 130
Nodes 3
Edges 2
Edge Density 0.007
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Klein Brak
Point
Freq
Time (H:M)
Spectral Density
Period (h)

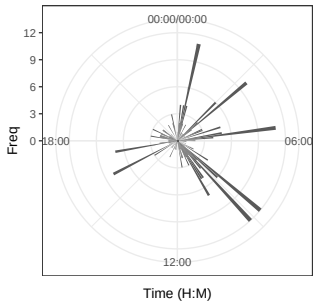
ID: 25867

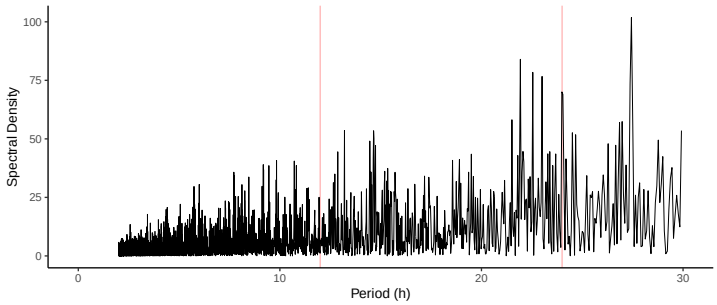
Poroderma africanum , female , 93 cm TL



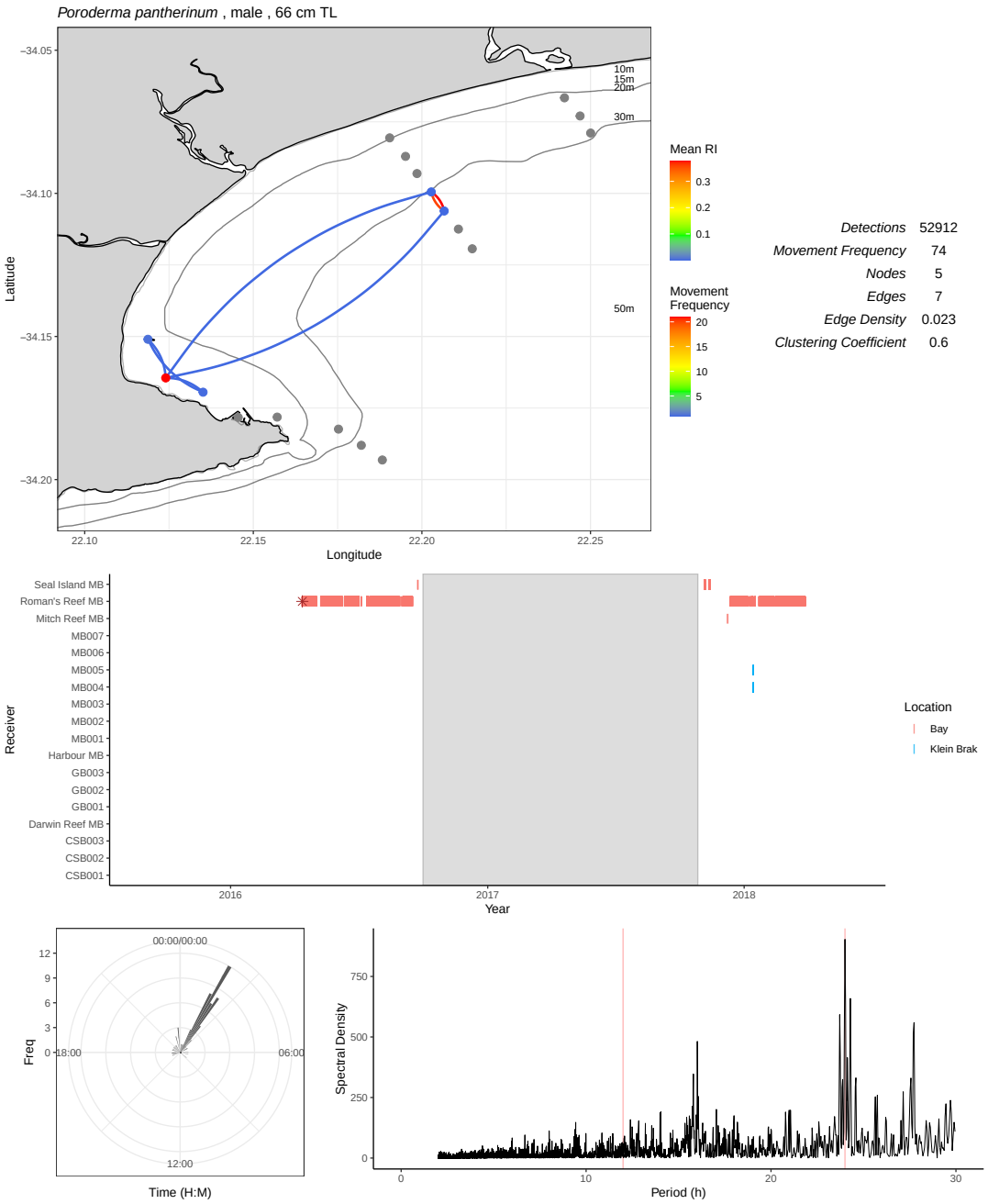
Detections	5849
Movement Frequency	235
Nodes	6
Edges	9
Edge Density	0.029
Clustering Coefficient	0.429





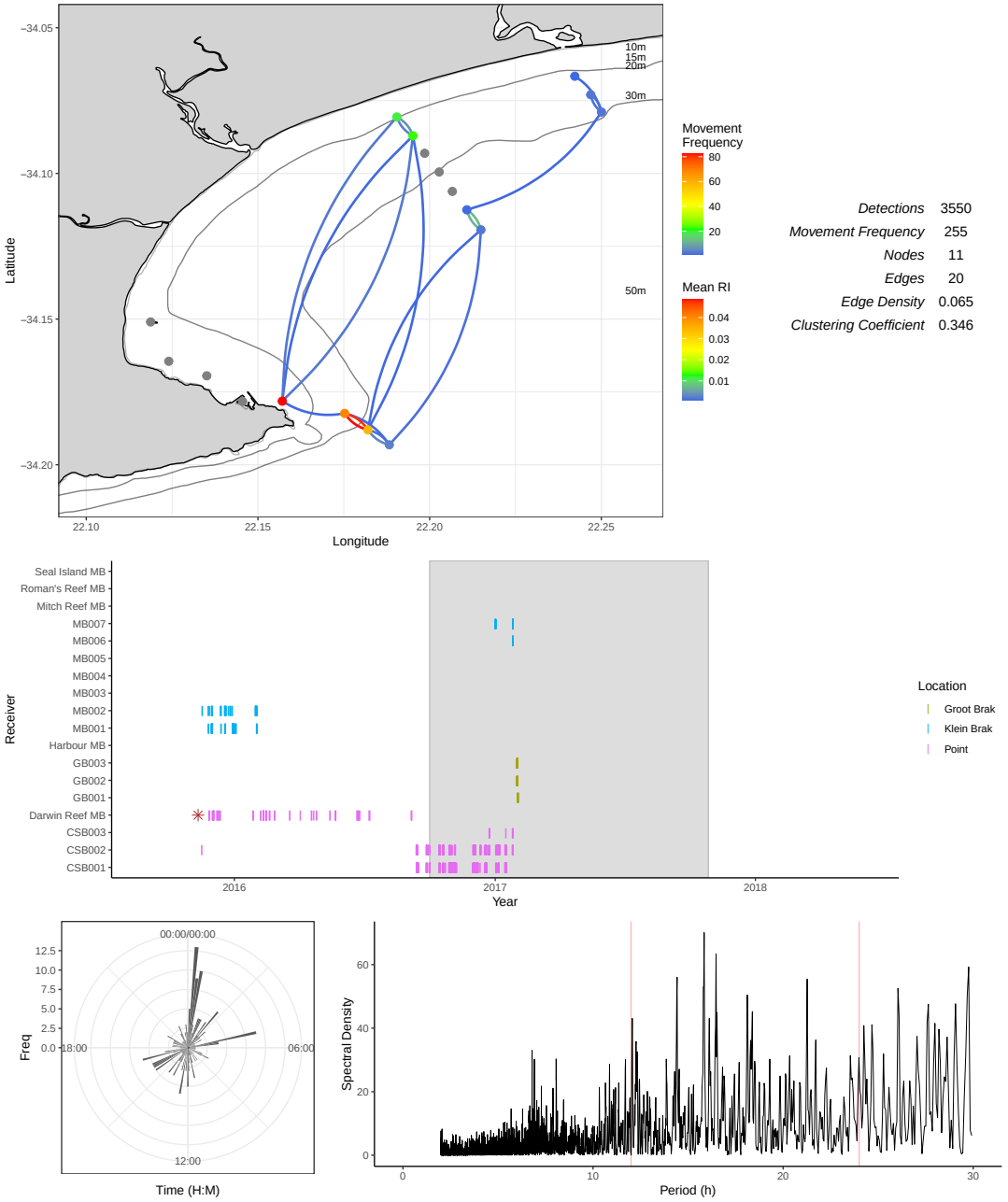


ID: 25868

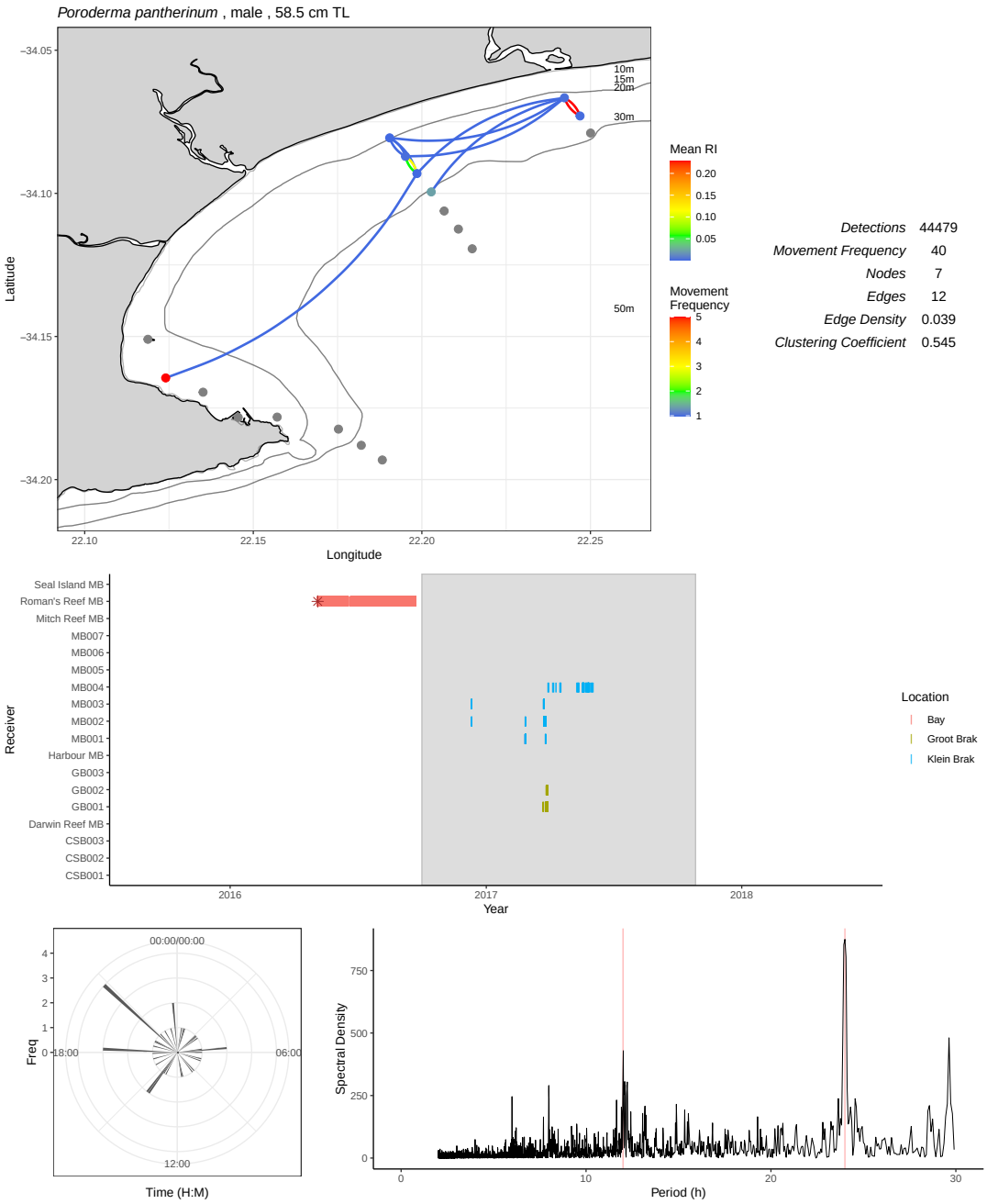

Poroderma pantherinum , male , 66 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 52912
Movement Frequency 74
Nodes 5
Edges 7
Edge Density 0.023
Clustering Coefficient 0.6
Receiver
Year
Location
Bay
Klein Brak
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25870

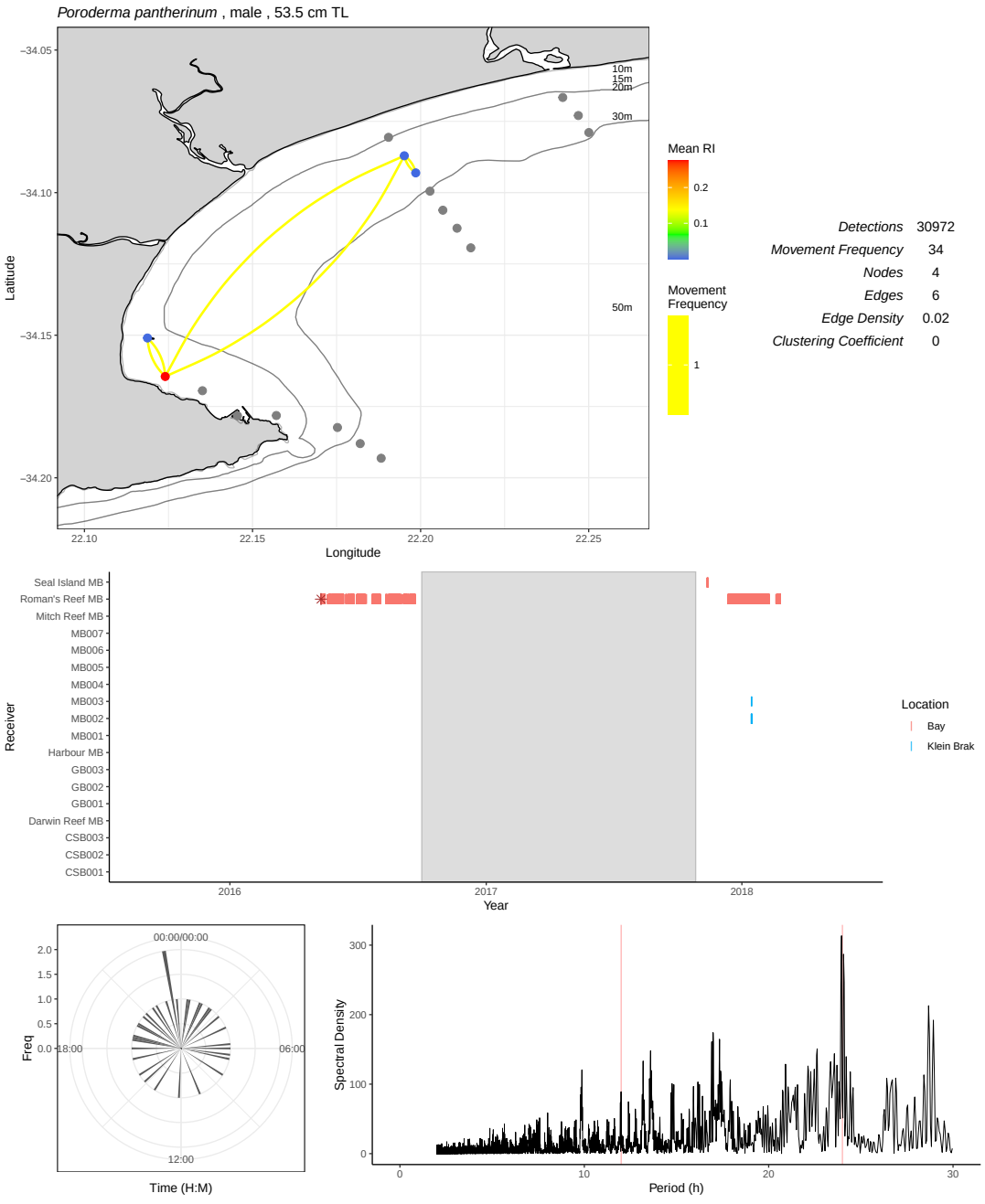
Poroderma africanum , male , 94.5 cm TL



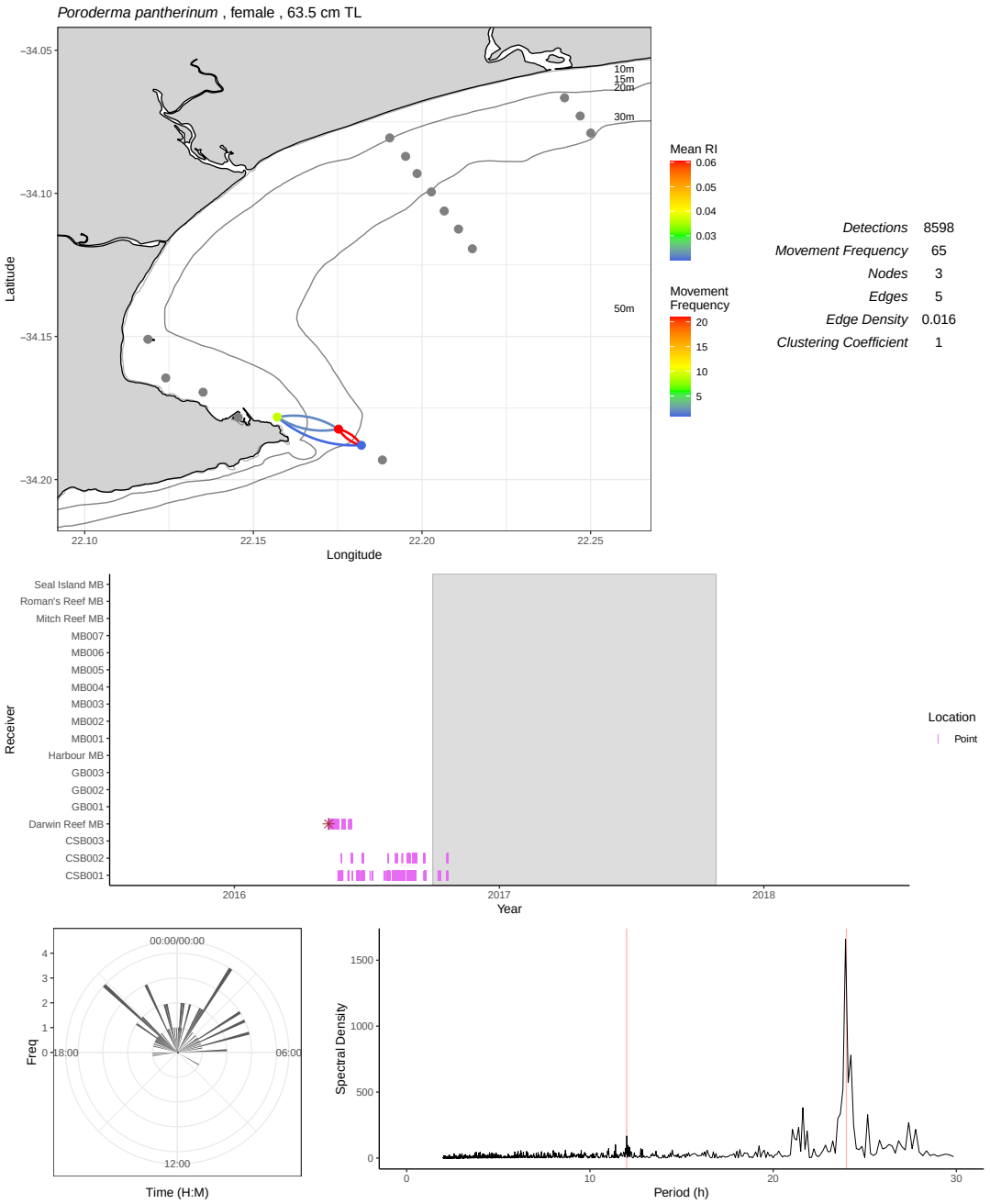
ID: 25871


Poroderma pantherinum , male , 58.5 cm TL
Latitude
Longitude
−34.05
−34.10
−34.15
−34.20
22.10
22.15
22.20
22.25
10m
15m
20m
30m
50m
Mean RI
0.20
0.15
0.10
0.05
Movement Frequency
5
4
3
2
1
Detections 44479
Movement Frequency 40
Nodes 7
Edges 12
Edge Density 0.039
Clustering Coefficient 0.545
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
2016
2017
2018
Year
Location
Bay
Groot Brak
Klein Brak
Freq
00:00/00:00
06:00
12:00
18:00
Time (H:M)
Spectral Density
750
500
250
0
10
20
30
Period (h)

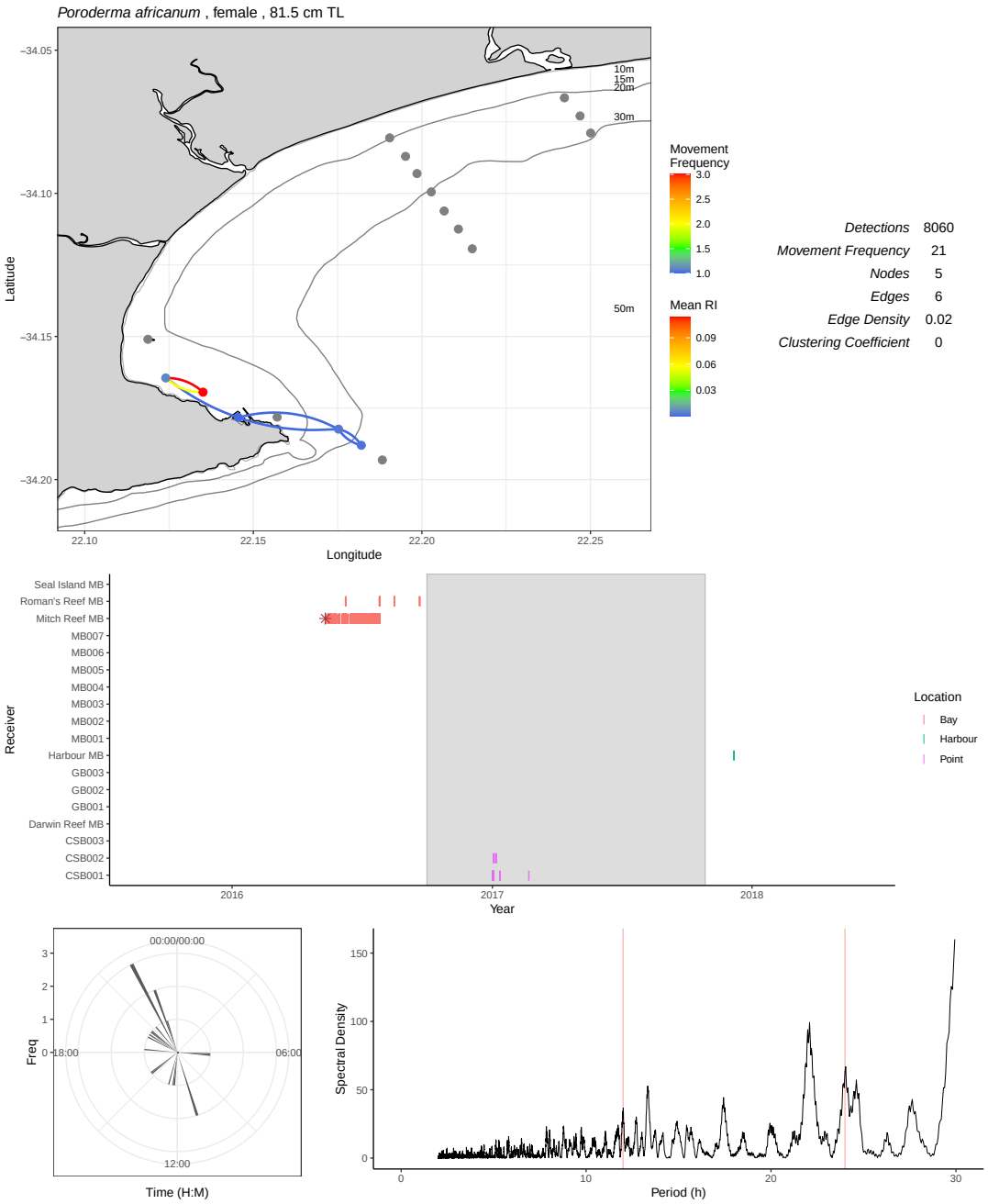
ID: 25873


Poroderma pantherinum , male , 53.5 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
0.2
0.1
Movement Frequency
1
Detections 30972
Movement Frequency 34
Nodes 4
Edges 6
Edge Density 0.02
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Bay
Klein Brak
Freq
Time (H:M)
Spectral Density
Period (h)

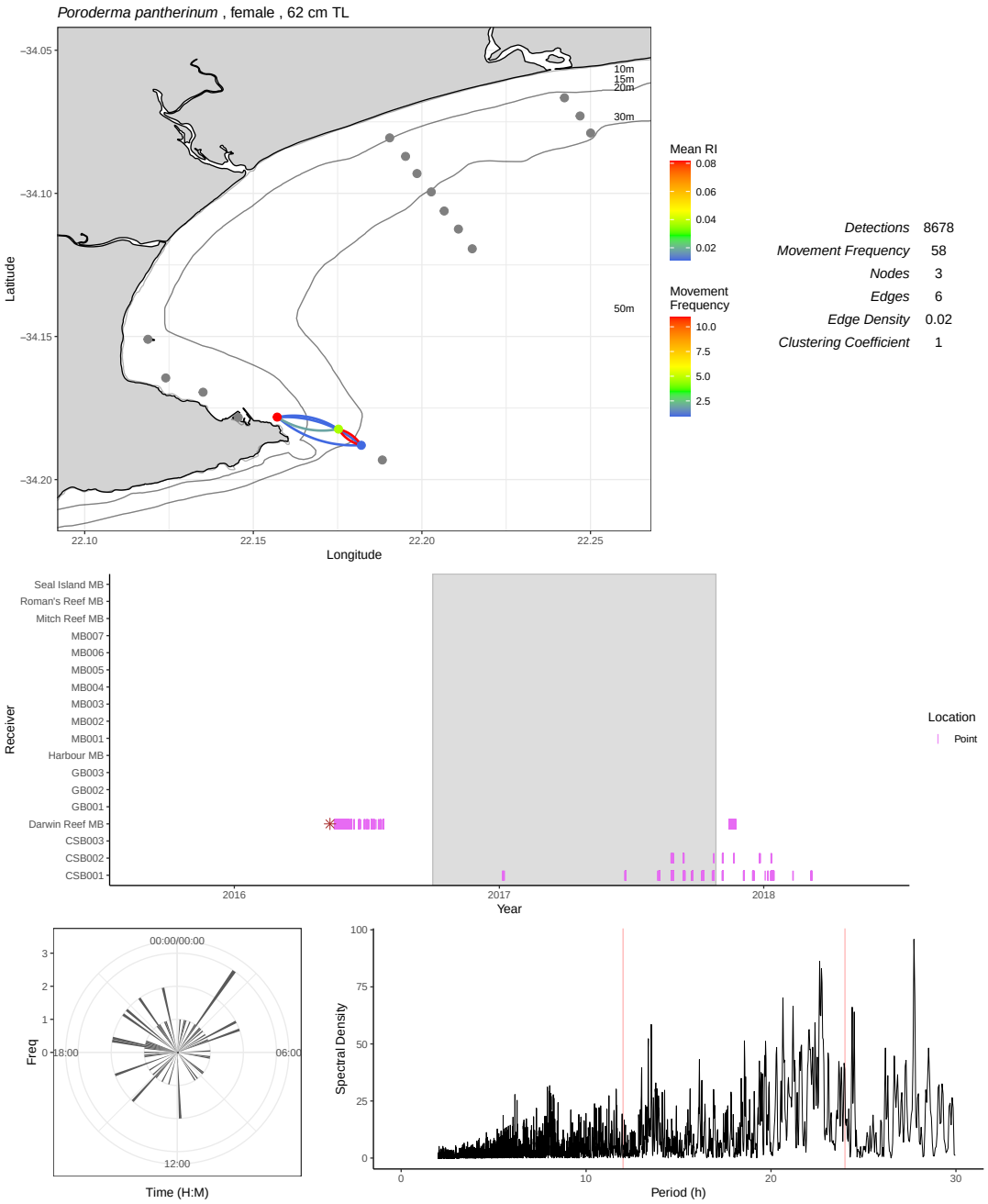
ID: 25874


Poroderma pantherinum , female , 63.5 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 8598
Movement Frequency 65
Nodes 3
Edges 5
Edge Density 0.016
Clustering Coefficient 1
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Point
Freq
Time (H:M)
Spectral Density
Period (h)

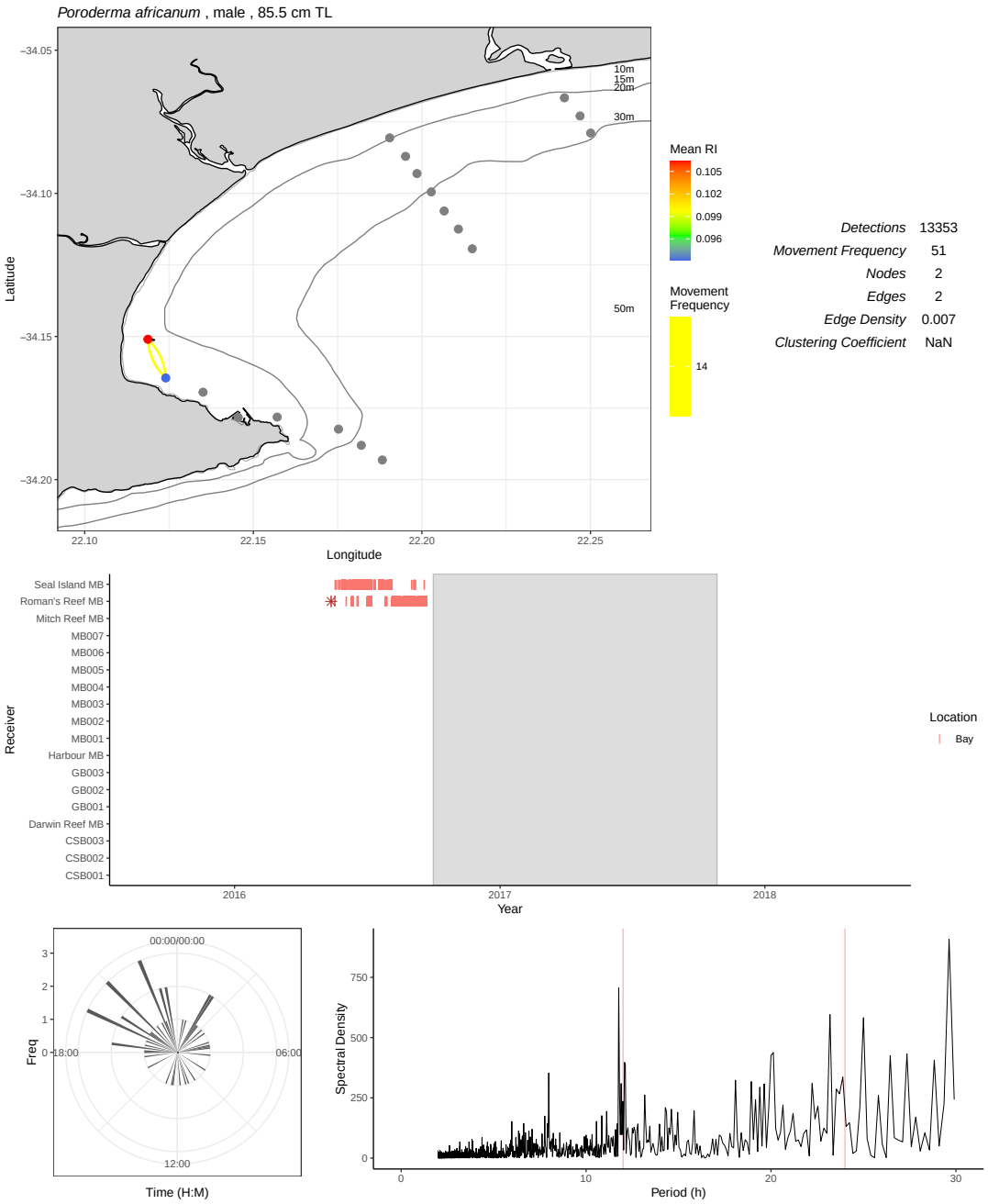
ID: 25875


Poroderma africanum , female , 81.5 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Movement Frequency
Mean RI
Detections 8060
Movement Frequency 21
Nodes 5
Edges 6
Edge Density 0.02
Clustering Coefficient 0
Receiver
Year
Location
Bay
Harbour
Point
Freq
Time (H:M)
Spectral Density
Period (h)

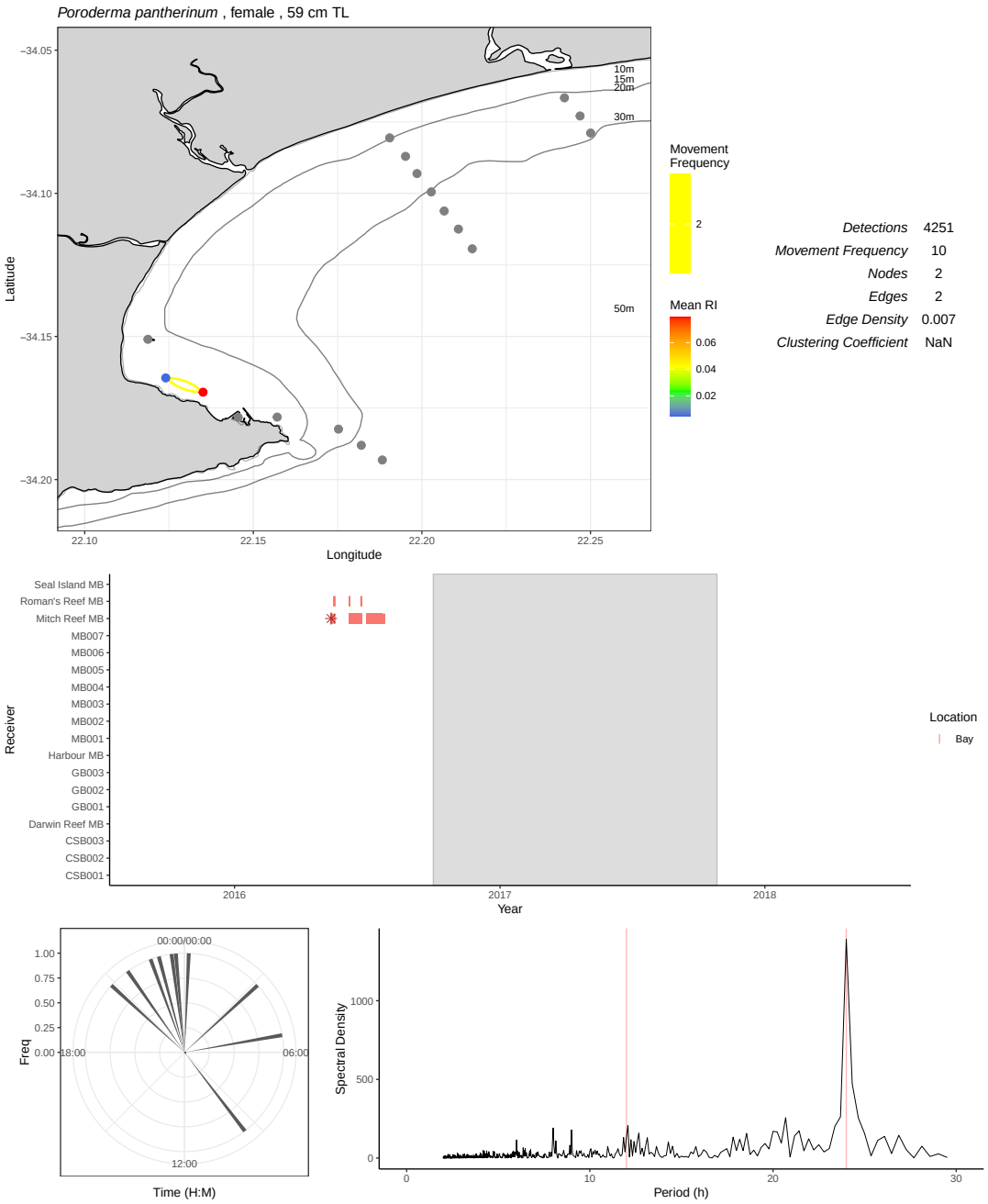
ID: 25879


Poroderma pantherinum , female , 62 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 8678
Movement Frequency 58
Nodes 3
Edges 6
Edge Density 0.02
Clustering Coefficient 1
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
Darwin Reef MB
Harbour MB
Year
Location
Point
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25880

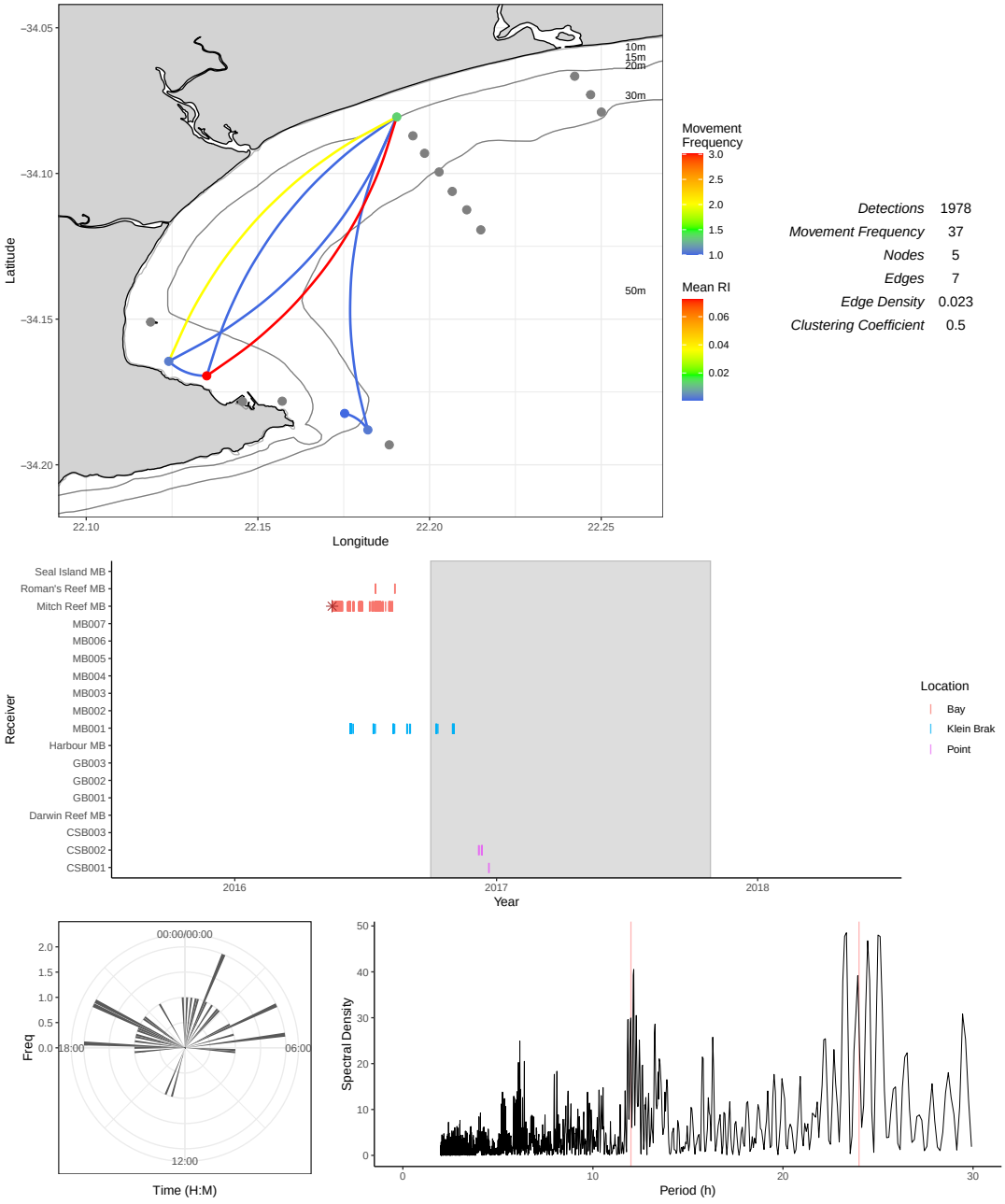

Poroderma africanum , male , 85.5 cm TL
Latitude
Longitude
−34.05
−34.10
−34.15
−34.20
22.10
22.15
22.20
22.25
10m
15m
20m
30m
50m
Mean RI
0.105
0.102
0.099
0.096
Movement Frequency
14
Detections 13353
Movement Frequency 51
Nodes 2
Edges 2
Edge Density 0.007
Clustering Coefficient NaN
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
2016
2017
2018
Year
Location
Bay
Freq
00:00/00:00
06:00
12:00
18:00
Time (H:M)
Spectral Density
Period (h)

ID: 25881


Poroderma pantherinum , female , 59 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Movement Frequency
Mean RI
Detections 4251
Movement Frequency 10
Nodes 2
Edges 2
Edge Density 0.007
Clustering Coefficient NaN
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
Darwin Reef MB
Harbour MB
Year
Location
Bay
Freq
Time (H:M)
Spectral Density
Period (h)

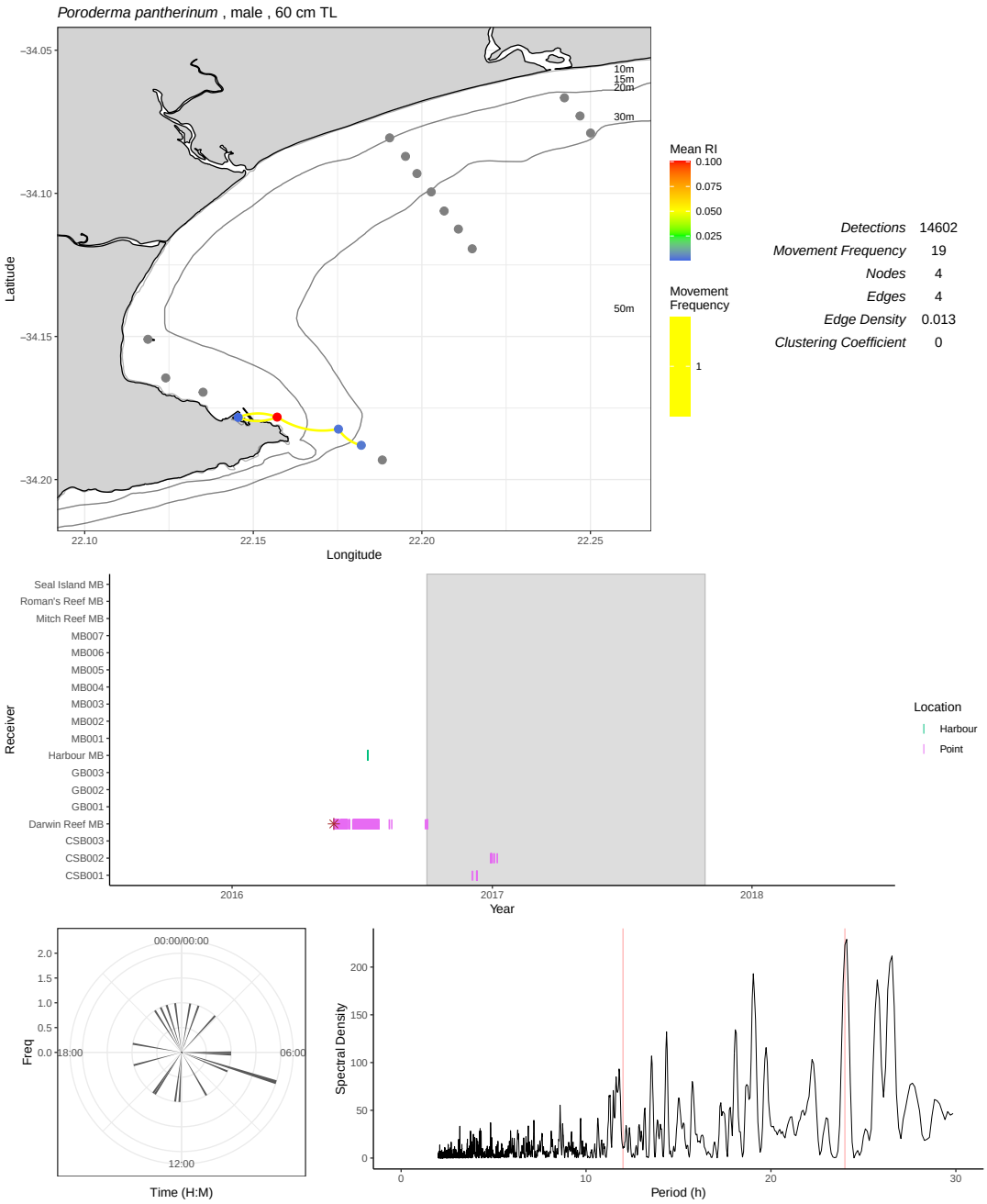
ID: 25882

Poroderma pantherinum , female , 62 cm TL

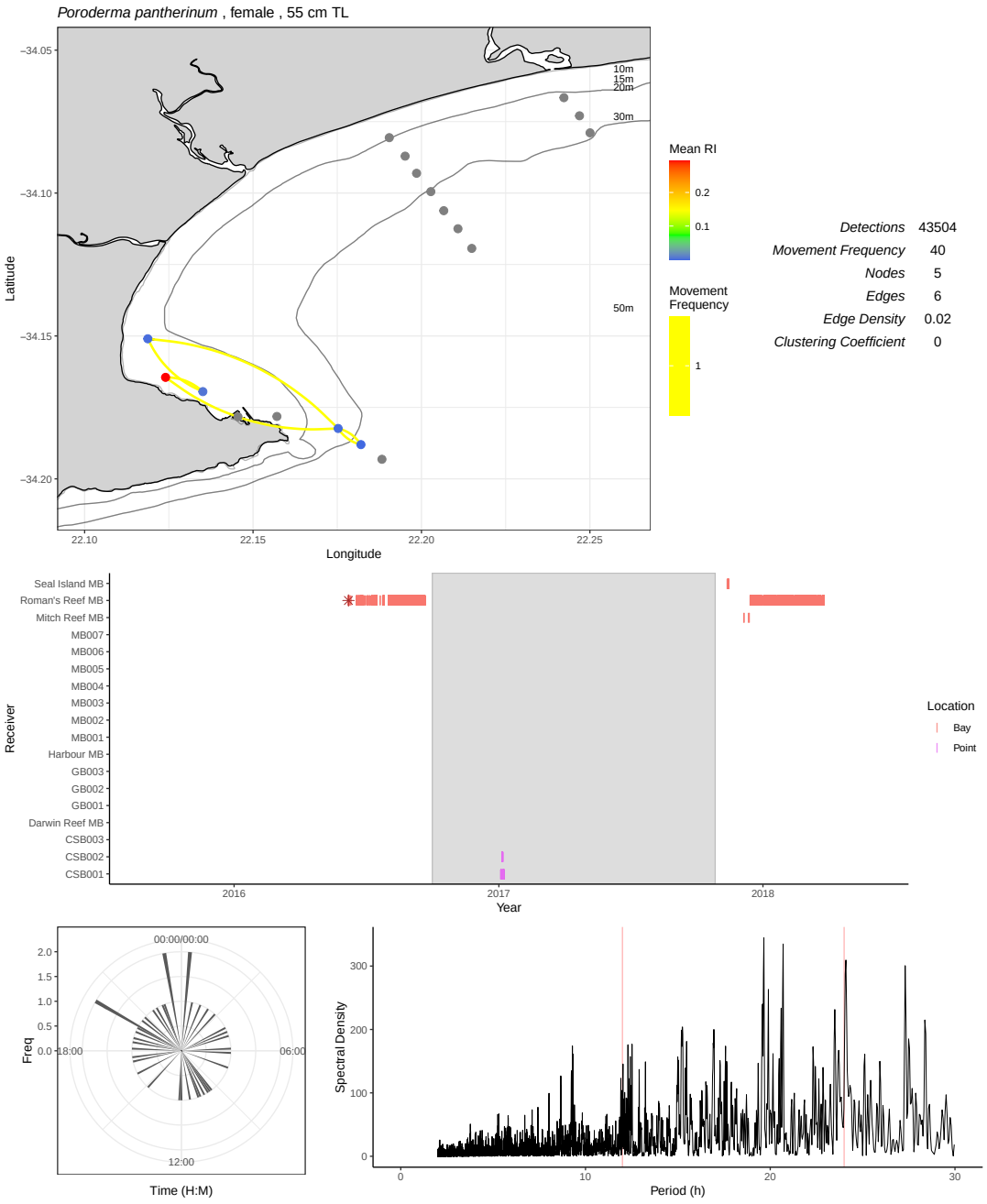


Detections	1978
Movement Frequency	37
Nodes	5
Edges	7
Edge Density	0.023
Clustering Coefficient	0.5

ID: 25883


Poroderma pantherinum , male , 60 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
0.100
0.075
0.050
0.025
Movement Frequency
1
Detections 14602
Movement Frequency 19
Nodes 4
Edges 4
Edge Density 0.013
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
MB007
MB006
MB005
MB004
MB003
MB002
MB001
Harbour MB
GB003
GB002
GB001
Darwin Reef MB
CSB003
CSB002
CSB001
Year
Location
Harbour
Point
Freq
Time (H:M)
Spectral Density
Period (h)

ID: 25884


Poroderma pantherinum , female , 55 cm TL
Latitude
Longitude
10m
15m
20m
30m
50m
Mean RI
Movement Frequency
Detections 43504
Movement Frequency 40
Nodes 5
Edges 6
Edge Density 0.02
Clustering Coefficient 0
Receiver
Seal Island MB
Roman's Reef MB
Mitch Reef MB
Harbour MB
Darwin Reef MB
Year
Location
Bay
Point
Freq
Time (H:M)
Spectral Density
Period (h)